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# Flora of Guaramacal (Venezuela) II

## Gymnosperms, Angiosperms (Chloranthales, Magnoliids)

*L. J. Dorr*
*and*
*S. Miguel Niño*

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**ABSTRACT.** Dorr, L. J., and S. Miguel Niño. *Flora of Guaramacal (Venezuela) II: Gymnosperms, Angiosperms (Chloranthales, Magnoliids)*. Smithsonian Contributions to Botany, number 120, xii + 93 pages, 9 figures, 97 maps, 2024.—The present volume is a taxonomic study of the Gymnosperms and Angiosperms (Chloranthales and Magnoliids) that occur in Guaramacal National Park (officially Parque Nacional "General Cruz Carrillo en Guaramacal"), which protects the Ramal de Guaramacal, an outlier of the more extensive Cordillera de Mérida in the Venezuelan Andes. The park covers 215 km$^2$ in Trujillo and Portuguesa states and includes cloud forest and páramo found between 1,600 and 3,150 m elevation. In all, nine families, 23 genera, and 97 species are treated; the greatest species diversity occurs in Piperaceae (50 species), Lauraceae (31 species), and Chloranthaceae (7 species). The most species-rich genera treated in this volume are *Peperomia* (31 species), *Piper* (18 species), and *Ocotea* (12 species). Five species treated here were described from collections made in the park and are currently known only from Guaramacal. One new combination, *Piper morii* (Steyerm.) Dorr & S. M. Niño, is made.

**RESUMEN.** Dorr, L. J., and S. Miguel Niño. *Flora of Guaramacal (Venezuela) II: Gymnosperms, Angiosperms (Chloranthales, Magnoliids)*. Smithsonian Contributions to Botany, número 120, xii + 93 páginas, 9 figuras, 97 mapas, 2024.—El presente volumen es un estudio taxonómico de las Gimnospermas y Angiospermas (Chloranthales y Magnoliids) presentes en el Parque Nacional Guaramacal (oficialmente Parque Nacional "General Cruz Carrillo en Guaramacal"), el cual da protección al Ramal de Guaramacal y es una pequeña porción aislada de la extensa Cordillera de Mérida en los andes venezolanos. El parque cubre 215 km$^2$ de superfice entre los estados Trujillo y Portuguesa, incluye bosques nublados y páramos establecidos entre 1,600 y 3,150 metros de elevación. En total, se reportan nueve familias, 23 géneros y 97 especies, la mayor diversidad de especies ocurre en las familias Piperaceae (50 especies), Lauraceae (31 especies) y Chloranthaceae (7 especies). Los géneros más ricos en especies tratados en este volumen son *Peperomia* (31 especies), *Piper* (18 especies) y *Ocotea* (12 especies). Cinco especies tratadas aquí se describieron a partir de colecciones hechas en el parque y actualmente solo se conocen de Guaramacal. Se hace una nueva combinación, *Piper morii* (Steyerm.) Dorr & S. M. Niño.

Cover images (left to right): Figures 2G, 4E, 5F, 5E, and 8I.

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# Flora of Guaramacal (Venezuela) II

## Gymnosperms, Angiosperms (Chloranthales, Magnoliids)

*L. J. Dorr*[1]* *and S. Miguel Niño*[2]

## INTRODUCTION

This is the second volume of a multi-volume work that will treat all the vascular plants (~1,300 species) that are found in Guaramacal National Park (officially Parque Nacional "General Cruz Carillo en Guaramacal"). The park was created in 1988 to protect the Ramal de Guaramacal, an outlier of the more extensive Cordillera de Mérida in the Venezuelan Andes and an important watershed for the Boconó and Tucupido reservoirs at the southeastern base of these mountains. The park covers 215 km$^2$ in Trujillo and Portuguesa states and is primarily composed of very steep slopes between 1,600 and 3,150 m elevation. The two principal vegetation types found in the park, cloud forest and páramo, have been intensively studied from an ecological perspective (Cuello A., 2002, 2010; Cuello A. and Cleef, 2009a, 2009b, 2009c, 2011).

For each species or infraspecific taxon recognized here, the accepted name is given in bold type. In addition, the basionym (if different) is cited, along with homotypic and heterotypic synonyms that mostly have been used in Venezuelan botanical literature. These synonymies are intended to help the user understand the application of names within Venezuela. Hence, synonymies are not complete nor are they intended to be complete. References to standard Venezuelan floras and checklists such as the Flora de Venezuela (de Laubenfels, 1982; Steyermark, 1984), Flora of the Venezuelan Guayana (Berry et al., 1995, 1998, 1999, 2001, 2003, 2004, 2005), Flora y Vegetación del Estado Táchira (Bono, 1996), Catálago Anotado e Ilustrado de la Flora Vascular de los Llanos de Venezuela (Duno de Stefano et al., 2007), Catálogo de la Flora y Vegetación de los Valles de la Vertiente Occidental de los Andes de la Cordillera de Mérida (Bono, 2010), and Libro Rojo de la Flora Venezolana, ed. 2 (Huérfano et al., 2020) are included as these often provide more extensive descriptions and synonymies, and/or illustrations of the taxa treated here. Finally, names used in the two earlier enumerations of plants occurring in Guaramacal (Ortega et al., 1987; Dorr et al., 2000) are cited, but only when they differ from the name recognized in this volume.

Distributional statements are intended to be global, but detail by country-level political unit is reserved generally for South America. Although Mexico, Central America, and the West Indies are part of a broadly defined North America, we list them separately from the remaining parts of that continent. Country-level political units in South America are listed from north to south (and west to east). Distribution within Venezuela is alphabetical by state and federal district (Distrito Capital or Dependencias Federales) unless grouped into the major Andean Mountain chains within the country (i.e., Cordillera de Mérida, Sierra de Perijá, and Cordillera de la Costa), within

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which the sequence also is alphabetical. The Distrito Federal was abolished in 1999 and subdivided into the Distrito Capital and Vargas state. For the most part, earlier distribution records for the Distrito Federal correspond to the Distrito Capital and we use the latter in the text. Vargas occupies a relatively small land area on the Caribbean coast, the principal localities being the port of La Guaira and Maiquetía airport, and when these localities are part of a taxon's distribution, we have used Vargas. The maps are intended to quickly convey distributions within Venezuela, and a single dot is placed in the center of the state or federal district for which we have a record of occurrence. Maps in this volume are adapted from Dorr (2014) and Canelón et al. (2024). Boundary representations are not necessarily authoritative. Localities within the park have been simplified from those given on herbarium labels; the north slope of Guaramacal faces Boconó and the south slope faces the Venezuelan llanos. The Páramo de Guaramacal is the highest area (3,000–3,150 m elevation) within the park and is ± located in the park's geographical center (Figure 1A). The Fila de Agua Fría (2,600–2,800 m) is the highest peak to the northeast of the Páramo de Guaramacal, whereas the Páramo del Pumar (2,600 m) is an unusually low and interesting páramo on an exposed ridge to the southwest of the Páramo de Guaramacal (Figure 1B–D). Other named localities are described in Dorr et al. (2000; see also Figure 1E–H). Elevations cited are for park records and are not to be interpreted as the total elevational

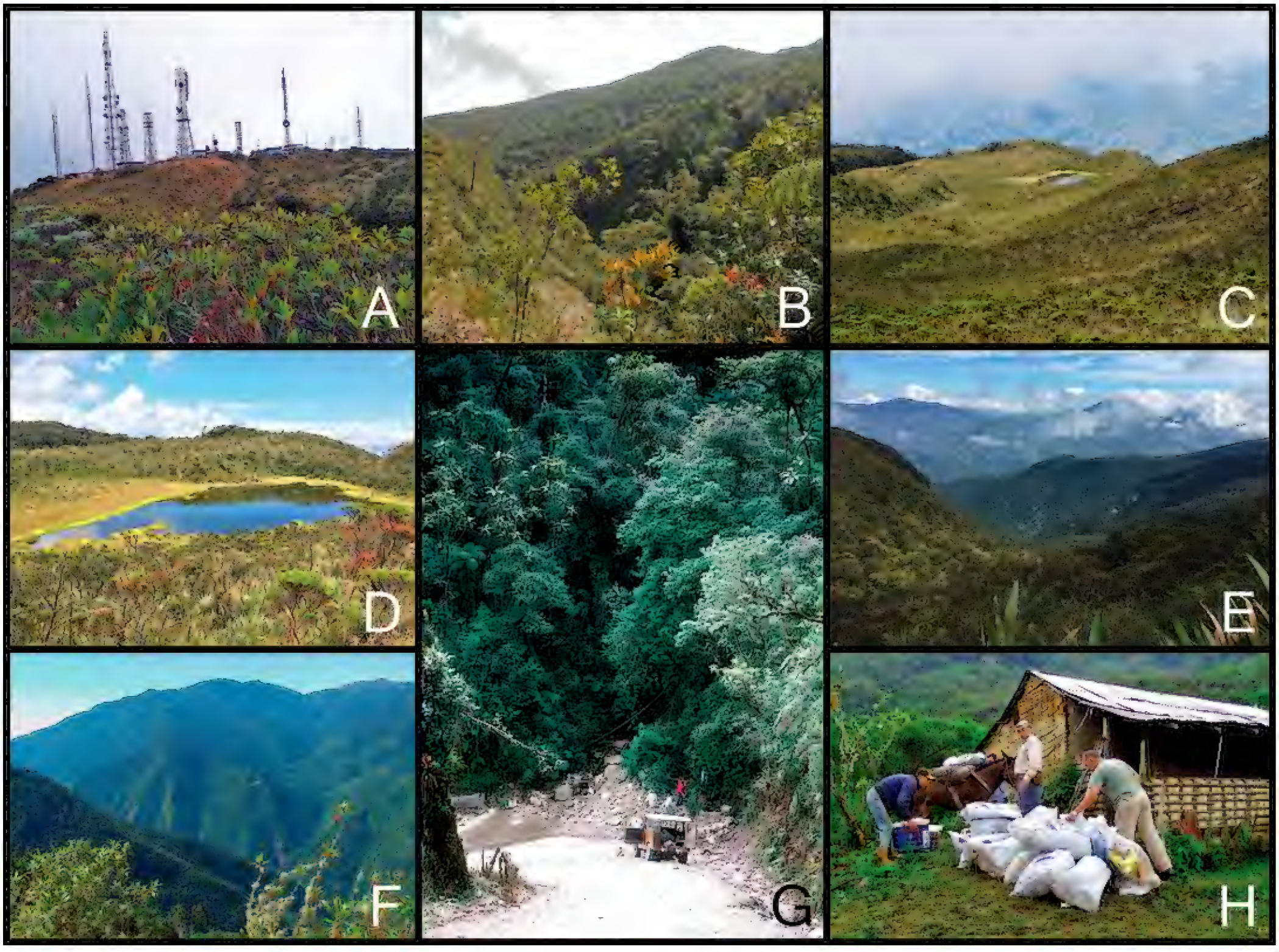



**FIGURE 1. A.** Antennas in the Páramo de Guaramacal. **B.** Cloud forest–subpáramo transition in Sector El Pumar. **C.** Páramo El Pumar with the Laguna del Pumar in the distance. **D.** Laguna del Pumar. **E.** Cloud forest on the north slope of Guaramacal with Parque Nacional Dinira in the distance. **F.** Quebrada (Qda.) Honda, south slope of Guaramacal. **G.** Qda. Jirajara, south slope of Guaramacal (Boconó–Guaramacal road). **H.** Casa Vicuyal, north slope of Guaramacal, with guardaparques Ramón Caracas (center) and Luis Briceño† (right) helping to break camp. (A–E, photographer D. Canelón; F–H, photographer L. J. Dorr).

range of a taxon. Also, elevations cited are taken from labels on specimens and rounded to 50 m intervals.

Common names cited in this flora are those that were communicated to us by the people living or working in the park. Likewise, the uses of plants that are presented here were provided to us by the people living or working in the park, notably our excellent guide and frequent field companion Ramón Caracas.

References are selective. Monographs and revisions are cited as are papers that provide the justification for our phylogenetic circumscription of a family or genus. Regional treatments of families and genera are cited only when they concern taxa found in Venezuela or neighboring Colombia.

## Abbreviations and Commonly Used Symbols

| | |
|---|---|
| aff. | affinis (i.e., akin to, bordering) |
| Art. | Article (see ICN) |
| auct. | auctorum (i.e., in the sense of a subsequent author and not the original author) |
| diss. | dissertation |
| ed., eds. | editor, editors |
| e.g. | exempli gratia (i.e., for example) |
| f. | forma (i.e., form) |
| fig., figs. | figure, figures |
| fol. | folio |
| ibid. | ibidem (i.e., the same, in the same place) |
| ICN | International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al., 2018) |
| i.e. | id est (i.e., that is) |
| in sched. | in schedula (i.e., on a specimen label) |
| nom. cons. | nomen conservandum (i.e., name conserved by the ICN) |
| nom. illeg. | nomen illegitimum (i.e., illegitimate name) |
| nom. illeg. superfl. | nomen illegitimum et superfluum (i.e., superfluous illegitimate name) |
| nom. nov. | nomen novum (i.e., replacement name) |
| nom. nud. | nomen nudum (i.e., designation of a new taxon published without a description or diagnosis or reference to a description or diagnosis) |
| p., pp. | page, pages |
| p.p. | pro parte (i.e., partly, in part) |
| Qda. | Quebrada (i.e., ravine) |
| qu. | quarto |
| sect. | section |
| s.l. | sensu lato (i.e., in the broad sense) |
| sp. | species |
| sphalm. | sphalmate (i.e., by mistake, mistakenly) |
| s. str. | sensu strictu (i.e., in the strict sense) |
| stat. et nom. nov. | status et nomen novum (i.e., replacement name at new rank) |
| subgen. | subgenus |
| subsect. | subsection |
| subsp. | subspecies |
| syn. nov. | synonymon novum (i.e., new synonym) |
| t., tt. | tabula, tabulae (i.e., plate, plates) |
| var. | variety |
| viz. | videlicet (i.e., it may be seen, or namely) |
| ♦ | signifies that a taxon (or its basionym) was described from material collected in Guaramacal National Park |
| • | signifies that a taxon is an introduced element in the flora of Guaramacal |
| = | heterotypic synonym (i.e., synonym based on different type) |
| ≡ | homotypic synonym (i.e., synonym based on the same type) |
| ± | more or less |
| ≥ | equal to or more than |
| > | greater than |
| < | less than |
| ≤ | equal to or less than |
| × | cross or times (used with numbers) |
| † | deceased |

# GYMNOSPERMS

## Podocarpaceae

L. J. DORR AND S. MIGUEL NIÑO

Dioecious or rarely monoecious trees or shrubs; evergreen; resinous. Leaves decussate, subopposite, or spirally arranged, simple, entire, scalelike or needlelike (not our species), linear, lanceolate, or ovate. Staminate (pollen) cones catkin-like, solitary or clustered, terminal or axillary, sessile or pedunculate, cylindrical, each cone consisting of a narrow rachis and numerous spirally arranged microphylls, each microphyll bearing 2 inverted microsporangia (pollen sacs); pollen grains with 2(3) air bladders each, rarely 0. Pistillate (seed) cones usually solitary, terminal, or axillary, pedunculate or nearly sessile, with 1–several scales (bracts), each one with a single ovule; bracts and seed scales either completely reduced, modified as a swollen succulent and colored "receptacle" (*Podocarpus*), or ± well-developed with more seeds per cone. Seed (solitary) surrounded by a dry or succulent sarcotesta or epimatium (a specialized ovuliferous scale that bears and completely encloses a single inverted ovule); cotyledons 4, fused to form 2 double structures.

A family of ~18–20 genera and ~175–185 species found in tropical and temperate regions of the southern hemisphere and subtropical regions world-wide, including Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, Ecuador, Peru, Bolivia, Brazil, Chile, and Argentina), Africa, Madagascar, Asia, Australia, and the Pacific Islands. Three genera and 17 species are native to mountainous regions of Venezuela. In addition, *Dacrydium lycopodioides* Brongn. & Gris and *Podocarpus macrophyllus* (Thunb.) Sweet, native to New Caledonia and eastern and southeastern Asia respectively, are cultivated in Venezuela. The former species is sometimes naturalized.

References. Schnee (1944); Buchholz and Gray (1957); Veillon (1962); de Laubenfels (1982); Torres-Romero (1988); Page (1990); Kelch (1997, 1998); Conran et al. (2000); Sinclair et al. (2002); Biffin et al. (2011, 2012); Knopf et al. (2012); Farjon (2017).

### KEY TO THE GENERA OF PODOCARPACEAE

1a. Leaves alternate, spiral, or subopposite, 3–15 cm long; branches striate to the apex . . . . . ***Podocarpus***

1b. Leaves opposite or subopposite (our species), decussate, 0.7–2.3 cm long; branches with encircling leaf scars . . . . . ***Retrophyllum***

## *Podocarpus* L'Hér. ex Pers.

*Podocarpus* L'Hér. ex Pers., Syn. Pl. 2(2): 580. 1807, nom. cons.
*Margbensonia* A. V. Bobrov & Melikyan, Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 103: 59. 1998.

Dioecious trees (our species) or shrubs. Leaves alternate, spiral, or subopposite, usually linear-lanceolate or linear-elliptic to elongate, midrib ± conspicuous below. Staminate (pollen) cones solitary or clustered on leafy branches, lateral, sessile or on a naked peduncle. Pistillate (seed) cones usually solitary, on leafy branches, lateral, borne on a naked peduncle; "receptacle" fleshy with 2 or more bracts holding an ovule. Seeds completely covered by an epimatium.

A tropical, subtropical, and southern temperate genus of ~115 species found in Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, Ecuador, Peru, Bolivia, Brazil, Chile, and Argentina), Africa, Madagascar, Asia, Australia, and the Pacific Islands. Approximately 12 species occur in Venezuela.

REFERENCES. Buchholz and Gray (1948); de Laubenfels (1985).

***Podocarpus oleifolius*** D. Don, in Lambert, Descr. Pinus 2: [20]. 1824 ("*Oleifolia*"). *Nageia oleifolia* (D. Don) Kuntze, Revis. Gen. Pl. 2: 800. 1891.

FIGURE 2A

*Podocarpus macrostachyus* Parl., in de Candolle, Prodr. 16(2): 510. 1868 ("*macrostachya*"). *Nageia macrostachya* (Parl.) Kuntze, Revis. Gen. Pl. 2: 800. 1891. *Podocarpus oleifolius* var. *macrostachyus* (Parl.) J. Buchholz & N. E. Gray, J. Arnold Arbor. 29: 140. 1948; de Laubenfels, Fl.

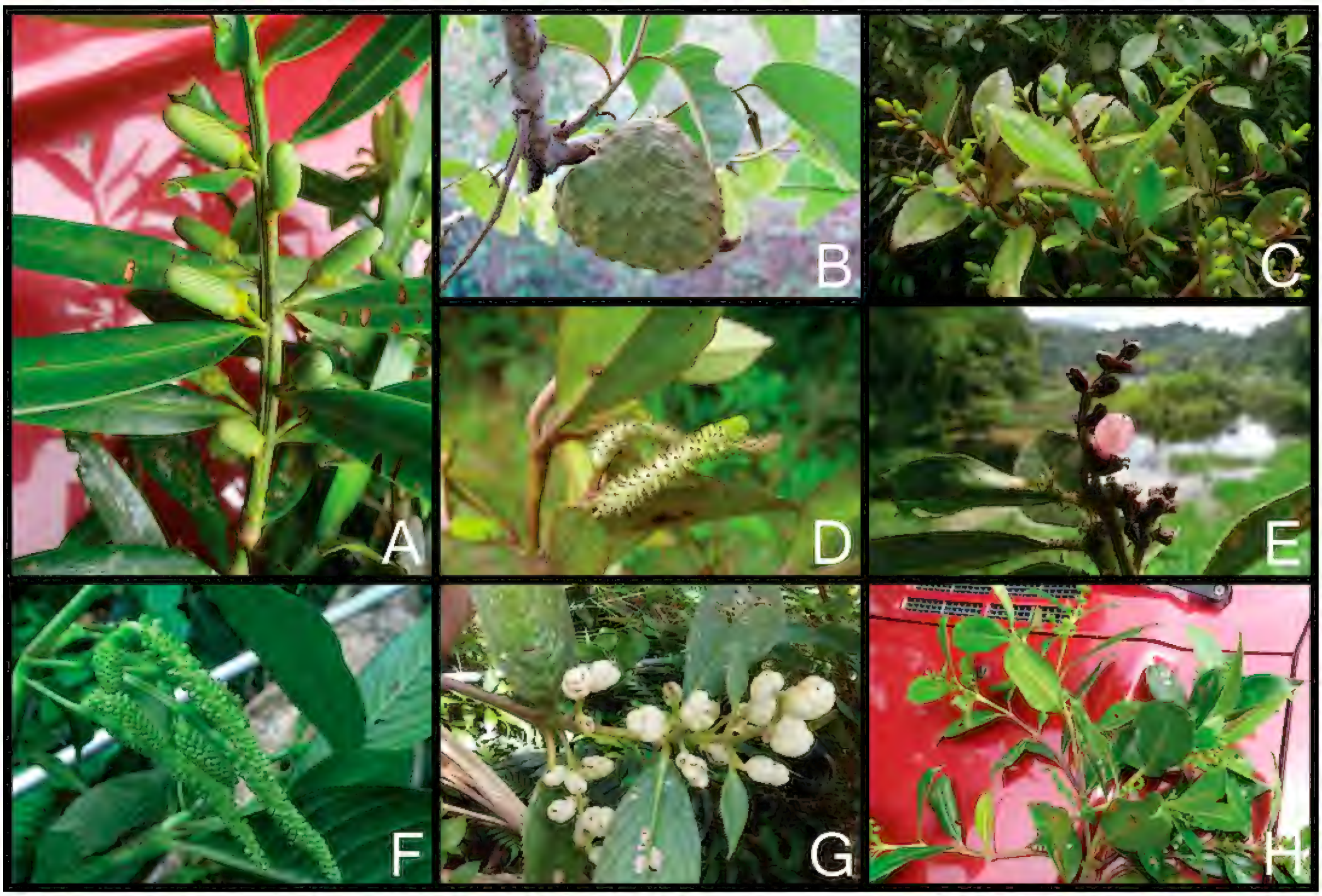



**FIGURE 2. A.** Podocarpaceae, *Podocarpus oleifolius* D. Don. Staminate cones. **B.** Annonaceae, *Annona mucosa* Jacq. Fruit. **C–E.** Chloranthaceae, *Hedyosmum gentryi* D'Arcy & Liesner. C. Habit. D. Staminate inflorescence. E. Fruit. **F, G.** *H. goudotianum* Solms var. *goudotianum*. F. Staminate inflorescence. G. Fruit. **H.** *H. racemosum* (Ruiz & Pav.) G. Don. Female inflorescences. (A, photographer S. M. Niño; B, photographer L. J. Dorr; C–H, photographer D. Canelón).

Venez. 11(2): 19–23, fig. 4. 1982; Ortega et al., BioLlania 5: 32. 1987; Bono, Fl. Veg. Táchira 746. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 35–36. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 63. 2010.

*Podocarpus oleifolius* var. *trujillensis* J. Buchholz & N. E. Gray, J. Arnold Arbor. 29: 141. 1948; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 63. 2010. *Podocarpus oleifolius* subsp. *trujillensis* (J. Buchholz & N. E. Gray) Silba, J. Int. Conifer Preserv. Soc. 17(1): 17. 2010.

Trees, (3–)6–30 m tall; young branches striate to the apex, pith spongy, sometimes hollow; leaf buds globose, 4–6 mm in diameter. Leaves elliptic to oblong-lanceolate, 3–15 × 1–2 cm, midrib prominent below, revolute, glabrous; sessile or short petiolate. Staminate (pollen) cones pedunculate or sometimes sessile; peduncles when present 2–12 mm long. Pistillate (seed) cones axillary, pedunculate; peduncles 5–20 mm long; "receptacle" fleshy, ~10 mm long. Seeds ovoid, ~10 × 5 mm, glaucous, green turning red or brown at maturity.

Mexico, Central America, and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, known from the Andes (Lara, Mérida, Portuguesa, Táchira, and Trujillo) and the Cordillera de la Costa (Aragua and Distrito Capital; Map 1). In the park, found in cloud forest on both slopes of Guaramacal and on the Fila de Agua Fría; 1,800–2,800(–3,000) m.

The wood when cut has a pine-like odor (fide *Dorr et al. 7348* in sched.).

*Podocarpus pendulifolius* J. Buchholz & N. E. Gray also has been collected in Trujillo state. It is easily distinguished from our species by its pendant or drooping leaves.

**MAP 1.** Distribution of *Podocarpus oleifolius*.

## *Retrophyllum* C. N. Page

*Retrophyllum* C. N. Page, Notes Roy. Bot. Gard. Edinburgh 45: 379. 1988 [1989].

*Decussocarpus* de Laub., J. Arnold Arbor. 50: 340. 1969, nom. illeg.

Dioecious trees. Leaves opposite or subopposite, decussate, lanceolate to ± narrowly ovate, usually twisted to form a single plane. Staminate (pollen) cones usually lateral, 1–5(–8) together, potentially arranged in racemose inflorescences; individal cones ± pedicellate, cylindrical, ellipsoid, or ovoid; microsporophylls imbricate, spirally arranged, lanceolate; pollen 2-saccate. Pistillate (seed) cones solitary, sometimes paired, borne on new growth as specialized reproductive shoots, pedunculate; peduncles widened distally; cone axis with 6–8 sterile bracts subtending 1 fertile bract; fertile bract with basal half adnate to the epimatium; "receptacle" vestigial; ovule inverted. Seed without a beak.

A genus of six species found in South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil) and the Pacific Islands. Two species occur in South America, one of which is found in the Andes of Venezuela.

References. Gray and Buchholz (1948); Page (1988); Herbert et al. (2002); Mill (2016).

*Retrophyllum* is closely related to *Afrocarpus* (J. Buchholz & N. E. Gray) C. N. Page and *Nageia* Gaertn. The three genera form a monophyletic clade sister to *Podocarpus* (Herbert et al., 2002; Sinclair et al., 2002; Biffin et al., 2011, 2012). Mill (2016), however, observed that while *Retrophyllum* forms a monophyletic clade in molecular studies, it appears to be an unnatural genus morphologically. *Retrophyllum* as defined by Page (1988, 1990) is held together by a single character (viz., heterofacially flattened shoots), which although unique in extant Podocarpaceae also exists in fossil taxa and therefore evolved more than once in the past. Mill (2016) also observed that the large disparities in the morphology of the six species of *Retrophyllym* correlate with three geographically separate areas and that species-pairs are found in Papuasia and Melanesia, New Caledonia, and South America, respectively. Despite these morphological differences, Mill (2016) chose to treat the three groups as a single genus. The type of *Retrophyllym*, *R. vitiensis* (Seem.) C. N. Page (≡ *Podocarpus vitiensis* Seem.), belongs to the species-pair found in Papuasia and Melanesia.

*Decussocarpus* de Laub. is an illegitimate name because *Nageia*, a genus now restricted to Asia, was cited as a synonym in its protologue (see Turland et al., 2018; Art. 52.1). However, because de Laubenfels (1969) cited a type for *Decussocarpus* (i.e., *D. vitiensis* (Seem.) de Laub.), the genus *Decussocarpus* is not typified by the type of *Nageia* (see Turland et al., 2018; Art. 7.5). In any case, the type of *Retrophyllym* (i.e., *R. vitiense* (Seem.) de Laub.) has the same basionym (viz., *Podocarpus vitiensis* Seem.) as that of *Decussocarpus*.

***Retrophyllum rospigliosii*** (Pilg.) C. N. Page, Notes Roy. Bot. Gard. Edinburgh 45: 380. 1988 [1989]. *Podocarpus rospigliosii* Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 8: 273. 1923 ("*Rospigliosii*"). *Decussocarpus rospigliosii* (Pilg.) de Laub., J. Arnold Arbor. 50: 347. 1969; de Laubenfels, Fl. Venez. 11(2): 9–11, fig. 1. 1982; Ortega et al., BioLlania 5: 32. 1987; Bono, Fl. Veg. Táchira 746. 1996; Huérfano et al., Libro Rojo Fl. Venez., ed. 2, 200. 2020. *Nageia rospigliosii* (Pilg.) de Laub., Blumea 32: 211. 1987.

Trees, 5–35 m tall; leaf scars encircling branches. Leaves subopposite, lanceolate or ovate-lanceolate, different sizes depending on location (and age) on a tree, those on lower branches 1–2.3 × 0.3–0.6 cm, while those on higher and more exposed branches 0.7–1.4 × 0.5 cm, narrowed abruptly to an acute-acuminate spinose apex; sessile. Staminate (pollen) cones 8–10 × 2.5 mm, solitary or in groups of up to 3. Pistillate (seed) cones terminal on specialized, lateral reproductive shoots, solitary. Seed obovoid, to 2.5 cm long (when dry), blue-black to red when ripe; bracts persistent.

South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, confined to the Andes (Mérida, Táchira, and Trujillo; Map 2). In the park, found near the Laguna de Los Cedros and along the trail from this laguna to the Boconó aqueduct; 1,850 m.

**MAP 2.** Distribution of *Retrophyllum rospigliosii.*

COMMON NAME. Pino laso.

## ANGIOSPERMS

### KEY TO THE FAMILIES OF CHLORANTHALES AND MAGNOLIIDS

1a. Perianth lacking or reduced to bracts in the base of the flower; plants generally aromatic; epiphytic or terrestrial . . . . . 2
2a. Terrestrial or epiphytic herbs, lianas, shrubs, or sometimes small trees (to 10 m tall); leaves alternate, verticillate (whorled), or opposite, often succulent; leaf margin entire; some terrestrial herbs with cilantro-like odor; flowers bisexual; ovary superior . . . . . ***Piperaceae***
2b. Trees, 2–15(–30) m tall; leaves opposite; leaf margin almost always dentate; plants with lemon-like fragrance; flowers unisexual; ovary inferior . . . . . ***Chloranthaceae***
1b. Perianth present; plants sometimes aromatic; terrestrial, never epiphytic . . . . . 3
3a. Leaves opposite; margin of leaf blade dentate . . . . . 4
4a. Leaves lemon-scented when crushed, margin irregularly dentate; fruit enclosed in a fleshy hypanthium; ovary inferior . . . . . ***Siparunaceae***
4b. Leaves not fragrant when crushed, margin dentate from middle to apex; fruit aggregate; ovary superior . . . . . ***Monimiaceae***
3b. Leaves alternate; margin of leaf blade entire . . . . . 5
5a. Petioles with stipular scars; inflorescence bracts 3, sheathing; flowers solitary . . . . . ***Magnoliaceae***
5b. Petioles without stipular scars; flowers solitary or borne in inflorescences without sheathing bracts . . . . . 6
6a. Plants not aromatic; stipules terminal; inflorescences pseudo-umbellate; flowers 2-merous, white ***Winteraceae***
6b. Plants aromatic; stipules not terminal; inflorescences cymose, paniculate, or flowers solitary; flowers 3-merous, yellow or greenish yellow . . . . . 7
7a. Leaves with curved, ascending secondary veins; inflorescences usually cymose, paniculate, or umbellate; flowers often small, ovary 1-locular; fruit borne on a cupule or with a thickened base, syncarpous. . . . ***Lauraceae***
7b. Leaves with straight or slightly curved secondary veins; flowers solitary or inflorescences cymose; flowers often conspicuous, ovary 1–many-locular; fruit not borne on a cupule nor with a thickened base, not syncarpous . . . . . ***Annonaceae***

## Annonaceae

S. MIGUEL NIÑO AND L. J. DORR

Trees and shrubs, rarely lianas; deciduous or evergreen; bark, leaves, and flowers often aromatic. Leaves simple, distichous, alternate, sometimes spiral, margin entire, glabrous or pubescent. Flowers solitary or in cymose inflorescences, bisexual or rarely unisexual, axillary, terminal or cauline, not showy, 3-merous; sepals 3–9 (sometimes 2–4), free or slightly attached at the base; petals 3–6, free; stamens numerous, spirally arranged; staminodes present or not; pollen grains shed in tetrads or polyads; pistils apocarpic, 1–many; ovary superior, usually 1–many ovules per carpel. Fruit fleshy or sometimes dry, comprised of 1–several carpels or a single structure (aggregate fruit). Seeds arillate or exarillate; endosperm abundant, ruminate.

This family has an extensive pantropical and subtropical distribution and includes ~2,150 species in ~111–130 genera. Found in North America (USA), Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay), Africa, Madagascar, Asia, Australia, and the Pacific Islands. In Venezuela, there are 21 genera and ~130 species of which 13 are endemic.

References. Wood (1958); Kessler (1993); Murillo A. (2001); Chatrou et al. (2012); Couvreur et al. (2012).

### KEY TO THE GENERA OF ANNONACEAE

1a. Flowers axillary; leaves and floral structures with abundant ferruginous hairs 0.5–2.5 mm long . . . . . ***Guatteria***

1b. Flowers supra-axillary or internodal; leaf bases and floral structures glabrous or with dispersed appressed hairs 0.1–0.5 mm long . . . . . 2

2a. Leaf blades 2–5.5 cm wide; petioles 0. 2–0.6 cm long; flowers borne on young branches; fruit globose, 1.2–4 cm in diameter . . . . . ***Trigynaea***

2b. Leaf blades 4–9 cm wide; petioles 1–2.5 cm long; flowers cauline or borne on young branches; fruit subglobose, 2–12(–20) cm in diameter. . . . . ***Annona***

## *Annona* L.

*Annona* L., Sp. Pl. 536. 1753.

*Rollinia* A. St.-Hil., Fl. Bras. Merid. [fol.] 1(1): 28. 1825 [1824]; ibid. [qu.] 1(1): 23. 1825 [1824].

Trees, shrubs, or lianas. Leaves glabrous or pubescent with stellate or bifurcated hairs. Flowers bisexual (rarely unisexual), solitary or in cymose inflorescences; pedicels bracteolate. Sepals 3, valvate, free or slightly attached at the base; petals 6 in 2 whorls or absent from the inner whorl, valvate or imbricate, fleshy, free; stamens numerous, spirally disposed; carpels numerous; ovary superior; 1 ovule per carpel. Fruit fleshy, aggregate, globose, ovoid, or irregularly ovoid. Seeds flattened, ellipsoid-obovoid, exarillate.

Native to North America (USA), Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay), and Africa (few species); cultivated and sometimes naturalized in the Paleotropics. *Annona* includes ~200 species of which ~19 species are found in Venezuela.

References. Maas and Westra (1992); Rainer (2007).

- ***Annona mucosa*** Jacq., Observ. Bot. 1: 16. 1764. *Rollinia mucosa* (Jacq.) Baill., Adansonia 8: 268. 1868; Maas, in Berry et al., Fl. Venez. Guayana 2: 458. 1995; Bono, Fl. Veg. Táchira 399. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 63. 2000 [2001]; Wingfield, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 347. 2007; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 167. 2010.

FIGURE 2B

Trees, 8–10(–25) m tall. Leaves narrowly elliptic, 10–25 × 4–9 cm, apex acuminate or cuspidate, pubescent above; petioles pubescent, 1–2.5 cm long. Inflorescences 1–3-flowered; pedicels 1.2–2.7 cm long, sparsely puberulent; sepals ovate, 3.5–4 × ~5 mm. Fruit green, subglobose, 2–12(–20) cm in diameter. Seeds brown, shiny, angular, 1.5–1.8 × 1–1.3 cm.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil); sometimes cultivated in the Paleotropics. Widespread in Venezuela (Amazonas, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Distrito Capital, Falcón, Lara, Mérida, Miranda, Portuguesa, Táchira, Yaracuy, and Zulia; Map 3). Cultivated and locally escaped near the lower boundaries of the park where it is found in coffee plantations and cloud forest near La Divisoria de la Concepción; 1,500–1,700 m.

Common Name. Chirimoya.

Use. The fruit is edible (fide *van der Werff et al. 7492* in sched.).

## *Guatteria* Ruiz & Pav.

*Guatteria* Ruiz & Pav., Fl. Peruv. Prodr. 85. 1794, nom. cons.

*Heteropetalum* Benth., J. Proc. Linn. Soc., Bot. 5: 69. 1861.

**MAP 3.** Distribution of *Annona mucosa*.

*Guatteriella* R. E. Fr., Acta Horti Berg. 12: 540. 1939.
*Guatteriopsis* R. E. Fr., Acta Horti Berg. 12: 540. 1939.

Trees or shrubs, rarely lianas; indumentum of simple hairs or absent. Leaves simple, entire, petiolate, estipulate, leaf blades with prominent midrib above. Inflorescences axillary, 1–few-flowered. Flowers bisexual, pedicellate; sepals 3, valvate, free or connate at base; petals 6, free, subequal, imbricate, almost always pubescent; stamens numerous; apex of connective truncate; carpels numerous, free; ovule 1, basal. Fruit apocarpous, consisting of numerous, indehiscent, fleshy stipitate monocarps; stipes frequently reddish; seeds ellipsoid, exarillate.

Mexico, Central America, the West Indies, and tropical South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, and Brazil). This Neotropical genus includes ~180(–300) species of which ~20 species occur in Venezuela.

REFERENCES. Erkens (2007); Erkens et al. (2007a, 2007b, 2009); Erkens and Maas (2008); Maas et al. (2015).

***Guatteria hirsuta*** Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 146. 1798.

*Guatteria pilosula* Planch. & Linden ex Triana & Planch., Ann. Sci. Nat., Bot., sér. 4, 17: 31. 1862; Wingfield, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 345. 2007; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 166. 2010.

*Guatteria laurina* Triana & Planch., Ann. Sci. Nat., Bot., sér. 4, 17: 32. 1862; Bono, Fl. Veg. Táchira 399. 1996.

*Guatteria persicifolia* Triana & Planch., Ann. Sci. Nat., Bot., sér. 4, 17: 33. 1862, nom. illeg.; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 166. 2010.

*Guatteria* sp. A; Dorr et al., Contr. U.S. Natl. Herb. 40: 63. 2000 [2001].

Trees, (2.5–)10(–30) m tall; young branches densely to sparsely pubescent. Leaves narrowly elliptic or narrowly oblong-elliptic, 5–15 × 2–4.5 cm, base acute to obtuse, apex acuminate with 5–20 mm long tips; secondary veins 8–15 on each side of the midrib, almost always with ferruginous hairs; petioles 2–4 mm long. Flowers in 1(–3)-flowered inflorescences in axils of leaves; pedicels 1–4 cm long, pubescent, ferruginous; sepals free, triangular or ovate-triangular, 6–10 mm long, apices pointed or rounded; petals 10–15 × 4–10 mm, green, turning yellowish-green at maturity. Fruit consisting of 10–100 monocarps, green, turning purplish to black at maturity.

Restricted to South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil). Fairly widespread in Venezuela (Apure, Barinas, Bolívar, Falcón, Lara, Mérida, Portuguesa, Táchira, Trujillo, and Zulia; Map 4). Found in coffee plantations and cloud forest on the lowermost slopes of Guaramacal near La Divisoria de la Concepción; 1,500 m.

## *Trigynaea* Schltdl.

*Trigynaea* Schltdl., Linnaea 9: 328. 1834 [1835].

Trees or shrubs; young branches pubescent with simple and short hairs, sometimes glabrate. Leaves simple; leaf blades elliptic, oblong, obovate, lanceolate, oblanceolate, or ovate. Flower buds globose to obovoid; flowers solitary on leafy new shoots, rarely cauliflorous or with several flowers on short shoots; pedicellate, pedicels internodal or supra-axillary; sepals valvate, connate at base and forming a bowl-shaped calyx; corolla white, cream, or yellow-green, sometimes ferruginous; petals free, ovate to elliptic, valvate; stamens 20–60, narrowly oblong, glabrous; anthers extrorse, apices with a conical connective; carpels 1–6; ovary ovoid to ellipsoid; ovules 6–12 per carpel, in two rows; stigmas globose, often 2-lobed. Fruit an aggregate or composed of 1 or 2 irregularly dehiscent monocarps; monocarps globose to obliquely pyrifom, puberulent or velutinous, sessile or stipitate; seeds 6–11(–12) per monocarp in 2 rows; calyx persistent.

**MAP 4.** Distribution of *Guatteria hirsuta*.

A tropical American genus of nine species restricted to South America (Colombia, Venezuela, Guyana, Suriname, Ecuador, Peru, Bolivia, and Brazil). A single species is known from Venezuela.

REFERENCES. Johnson and Mello-Silva (1993); Johnson and Murray (1995).

***Trigynaea duckei*** (R. E. Fr.) R. E. Fr., Ark Bot. 33A(9): 14. 1946 ("*Duckei*"); Wingfield, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 347, t. 59c. 2007. *Hornschuchia duckei* R. E. Fr., Acta Horti Berg. 12(1): 197. 1934 ("*Duckei*").

Trees or shrubs, 10–20 m tall; twigs sparingly pubescent, becoming glabrate. Leaf blades lanceolate, 5–20 × 2–5.5 cm, base rounded to cuneate, apex acuminate to attenuate or caudate, apical tip 2–4 cm long, sometimes curved, 6–15 secondary veins on each side of the midrib, sometimes 3-nerved at base or to ± midpoint of the leaf blade, glabrous or sparingly pubescent at the base and along the midrib, secondary veins slightly raised above and below; petioles short, 0.2–0.6 cm long. Flowers solitary on new shoots; pedicels short, 0.1–2.4 cm long; calyx 3–5 mm in diameter; corolla white or cream with appressed ferruginous hairs; petals coriaceous; carpels 2–5; ovaries 1.5–3 mm long. Fruit composed of 1 or 2 monocarps; monocarps globose, sometimes ovoid or compressed laterally, 1.2–4 cm in diameter.

Found in South America (Venezuela, Guyana, Ecuador, Peru, Bolivia, and Brazil). Venezuelan records are from the Andes (Mérida, Portuguesa, and Táchira) and the llanos (Apure; Map 5). Our material is from the lowermost south slopes of the park along the Camino Real from Paramito to Batatal; 1,600 m.

**MAP 5.** Distribution of *Trigynaea duckei.*

COMMON NAME. Negrito.

## CHLORANTHACEAE

S. MIGUEL NIÑO AND L. J. DORR

Monoecious or dioecious trees, shrubs, and herbs; aromatic essential oils abundant. Leaves simple, opposite, petiolate, with interpetiolar stipules; leaf margin generally serrate or toothed. Inflorescences in racemes, panicles, or spikes, axillary or terminal. Flowers small, unisexual or bisexual. Staminate flowers comprised of 1 stamen; anther dehiscent longitudinally by grooves or valves; anther connective variable in shape and size. Gynoecium (when present) comprised of a carpel (monomerous), superior or partially superior, with an ovule with apical placentation. Fruit fleshy, drupe or achene. Seeds with starch, embryo rudimentary, cotyledons 2, minute.

A pantropical family of four genera and ~75 species found in Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia, Brazil, and Paraguay), Madagascar, Asia, and the Pacific Islands. *Hedyosmum* Sw. is the only Neotropical genus in this family.

REFERENCES. Todzia (1993b); Doyle et al. (2003); Zhang and Renner (2003); Eklund et al. (2004).

### *Hedyosmum* Sw.

*Hedyosmum* Sw., Prodr. 5, 84. 1788.

Monoecious or dioecious trees and shrubs; aromatic; stems almost always with a persistent petiolar sheath. Leaves simple; petiolar sheaths and stipules distal to the margin of the sheath. Staminate inflorescences axillary or terminal with one or several spikes or clusters; staminate flowers sessile, ebracteolate; anther connective usually extended, acute or acuminate. Pistillate inflorescences terminal or axillary, with 1–several racemes or panicles subtended by a floral bract; perianth 3-lobed; ovary 1-locular, trigonous or ellipsoidal, inferior. Fruit a drupe, often multiple, almost always with concrescent fleshy bracts.

A primarily Neotropical genus of ~45 species found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia, Brazil, and Paraguay); one herbaceous species also occurs in Asia. Species diversity is greatest in the northern Andes. Twelve species are found in Venezuela.

REFERENCES. Todzia (1988); Antonelli and Sanmartín (2011); Doria et al. (2012); Martínez et al. (2013); Niño and Dorr (2019).

KEY TO THE SPECIES OF *HEDYOSMUM*

1a. Stems, leaves, and petiolar sheaths glabrous; fruit purplish or reddish black . . . . . 2
2a. Petiolar sheaths smooth to verrucose, glabrous to scurfy; stipular appendages lacking; fertile nodes with 1–3 cymules, each cymule 3–8-flowered. . . . . ***H. cuatrecazanum***

2b. Petiolar sheaths smooth or slightly rugulose; stipular appendages 2–4, caducous; fertile nodes with 2–10 cymules, each cymule 2–3-flowered. . . . . *H. gentryi*

1b. Stems, leaves, and petiolar sheaths or only one of them pubescent or with minute or dense vestiture; fruit white . . . . . 3

3a. Petiolar sheaths glabrous or with ciliate lines; leaf blades glabrous below . . . . . 4

4a. Leaf margin crenulate; pistillate inflorescences comprised of 4–12 cymules, each cymule 1–4-flowered; staminate inflorescences comprised of 1–2 opposite pairs of spikes terminating in a simple spike, peduncles 4–10 mm long . . . . . *H. crenatum*

4b. Leaf margin sharply serrate; pistillate inflorescences comprised of 5–30 cymules, each cymule 2–8-flowered; staminate inflorescences comprised of 1–3 spikes per node, sessile or on short peduncles 1–4 mm long. . . . . *H. racemosum*

3b. Petiolar sheaths tomentose and almost always scabrous to the touch; leaf blades scabrous below . . . . . 5

5a. Hairs abundant on the midrib and secondary veins of leaves; staminate inflorescences 1–5 cm long. . . . . *H. guaramacalense*

5b. Hairs dispersed on the midrib and secondary veins of leaves; staminate inflorescences 2.5–12.5 cm long. . . . . 6

6a. Leaf blades to 20 × 8.5 cm; petiolar sheaths with 2 fimbriate, caducous stipular appendages; staminate inflorescences comprised of 1–2 opposite pairs of spikes; pistillate inflorescences comprised of 4–16 cymules, each cymule 2–8-flowered . . . . . *H. goudotianum*

6b. Leaf blades to 14.5 × 5.5 cm; petiolar sheaths lacking stipular appendages; staminate inflorescences comprised of 1–3 opposite pairs of spikes; pistillate inflorescences comprised of 5–12 cymules, each cymule 4–7-flowered . . . . . *H. translucidum*

*Hedyosmum crenatum* Occhioni, Contr. Estud. Fam. Chloranthaceae 60. 1954.

Dioecious shrubs or trees, 2–8(–10) m tall; young stems quadrangular in cross-section, terete in age. Leaves narrowly elliptic or elliptic to slightly obovate, 5–10(–12) × 1.5–3 cm, base cuneate, margin crenulate, apex acuminate with a 0.2–0.8 cm long tip, glabrous; petioles 0.5–1.5 cm long; petiolar sheaths 1–1.5 cm long, slightly inflated, persistent, smooth or with 2 raised lines extending down from stipular processes, persistent, stipular appendages 1–2 mm long. Staminate inflorescences terminal or axillary, 1–2 opposite pairs of spikes, 5–8 cm long; anthers 1–2 mm long, green, connectives minute, 0.3–0.5 mm long. Pistillate inflorescences axillary or terminal, simple or branched racemes bearing 4–12 cymules, each cymule with 1–4 flowers. Mature fruit fleshy, white, 5–8 mm in diameter.

Endemic to northern South America (Colombia and Venezuela). In Venezuela, known from the Andes (Lara, Mérida, Táchira, and Trujillo) and the Sierra de Perijá (Zulia; Map 6). Found in cloud forest on both slopes of Guaramacal; (1,500–)1,950–2,900 m.

**MAP 6.** Distribution of *Hedyosmum crenatum.*

*Hedyosmum cuatrecazanum* Occhioni, Contr. Estud. Fam. Chloranthaceae 23. 1954, nom. nov. *Hedyosmum crassifolium* Cuatrec., Caldasia 3: 435. 1945, non *Hedyosmum crassifolium* Urb., Repert. Spec. Nov. Regni Veg. 24: 2. 1927.

Dioecious trees, 4–15(–30) m tall; young branches quadrangular in cross-section, terete in age. Leaves obovate or narrowly obovate to narrowly elliptic, 5–12 × 2–4.5 cm, base cuneate, margin crenate, apex acuminate with a 2–3 mm long tip, glabrous; petioles 0.2–1 cm long; petiolar sheaths 0.5–2.5 cm long, inflated, smooth to verrucose, glabrous to scurfy, without stipular appendages. Staminate inflorescences terminal or axillary spikes, 4–7 cm long; anthers 1.5–2.5 mm long, yellowish-green, connectives minute, 0.3–0.5 mm long. Pistillate inflorescences axillary or terminal, 1.5–3 cm long, comprised of 1–3 cymules, each cymule 3–8-flowered; flowers trigonous, 3–4.5 × 1–1.5 mm. Mature fruit globose, 1–1.5 cm in diameter, fleshy, purplish black.

South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, confined to the Andes (Trujillo; Map 7) where it is only known from collections made in Guaramacal. In the park, found in cloud forest on the north slope of Guaramacal; 2,000–2,350 m.

*Hedyosmum gentryi* D'Arcy & Liesner, Syst. Bot. 6: 84. 1981.
FIGURE 2C–E

Dioecious trees, 3–10 m tall; young branches quadrangular in cross-section, terete in age. Leaves obovate to elliptic, 5–12 × 2–4.5 cm, base broadly cuneate, margin serrate, apex slightly acuminate with a 1–6 mm long tip, glabrous; petioles 0.5–2 cm long;

**MAP 7.** Distribution of *Hedyosmum cuatrecazanum.*

**MAP 8.** Distribution of *Hedyosmum gentryi.*

petiolar sheaths 4–12 × 4–7 mm, slightly inflated, slightly rugulose with 2 subulate, entire stipular processes 0.3–1 mm long. Staminate inflorescences terminal or axillary racemes, 2–10 cm long; anthers 2–3 mm long. Pistillate inflorescences terminal or axillary, racemes or panicles, 2–10 cm long, comprised of 2–10 cymules, each cymule 2–3-flowered; flowers trigonous, 3–4 × 1.5–2.5 mm. Mature fruit fleshy, purple, brownish-maroon, or reddish, turning pink, trigonous, 4–5 mm in diameter.

Known from Central America (Panama) and South America (Colombia and Venezuela). In Venezuela, found in the Andes (Mérida, Portuguesa, Táchira, and Trujillo) and in the Cordillera de la Costa (Aragua, Falcón, Miranda, Monagas, and Yaracuy; Map 8). In the park found on the north slope along the Boconó–Guaramacal road; 1,650–2,600(–3,000) m.

Collections from the Venezuelan Guayana (Amazonas and Bolívar) that were referred to this species by Todzia (1988) were subsequently separated by her as *Hedyosmum intermedium* Todzia, which differs from *H. gentryi* in having 2–3 flowers (versus 1) per cymule.

***Hedyosmum goudotianum*** Solms, in de Candolle, Prodr. 16(1): 482. 1869 ("*Goudotianum*").

The nominate variety is the only one found in Venezuela.

***Hedyosmum goudotianum*** var. ***goudotianum***

FIGURE 2F,G

Dioecious trees, (2–)3.5–8 m tall; aromatic with citrus-like odor; young stems quadrangular in cross-section. Leaves ovate to elliptic, 5–20 × 3–8.5 cm, base cuneate, margin dentate, apex acuminate with a 0.5–1.5 cm long tip, slightly scabrous above and below; petioles 0.6–1.3 cm long; petiolar sheaths 0.5–3 × 0.4–1.5 cm, slightly inflated, smooth to asperous, glabrous to strigose, persistent, almost always quadrangular, grooved, sometimes with short hairs below the stipules, with 2 fimbriate, caducous appendices 1–3 mm long. Staminate inflorescences terminal or axillary, comprised of 1–2 pairs of opposite spikes, 1.3–8.5 cm long; anthers 1–2 mm long. Pistillate inflorescences axillary or terminal, racemes or panicles, 1.3–8.5 cm long, comprised of 4–16 cymules, each cymule 2–8-flowered; flowers trigonous, 1.5–3 × 1.5–2 mm. Mature fruit irregularly globose, 5–8 mm in diameter, fleshy, white, milky white, or greenish-white.

The nominate variety occurs in Central America (Costa Rica and Panama) and South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, it is restricted to the Andes (Táchira and Trujillo; Map 9). An understory tree in cloud forest

**MAP 9.** Distribution of *Hedyosmum goudotianum* var. *goudotianum.*

in the park where it is found on both slopes including near the Laguna de Aguas Negras and along the Boconó–Guaramacal road; 1,700–2,350 m.

The only other variety recognized, *Hedyosmum goudotianum* var. *mombachanum* Todzia, is restricted to Central America (Nicaragua). It can be distinguished from the nominate one by shorter internodes, more distantly spaced teeth on the leaf margin, and overlapping leaf sheaths.

♦ ***Hedyosmum guaramacalense*** S. M. Niño & Dorr, Harvard Pap. Bot. 24: 269, figs. 1, 2A. 2019.

FIGURE 3

*Hedyosmum* sp. A; Dorr et al., Contr. U.S. Natl. Herb. 40: 83. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 260. 2010.

Dioecious trees, 2–10 m tall; aromatic with a citrus-like odor; young stems quadrangular in cross-section, pubescent, petiolar sheaths persisting. Leaves elliptic or narrowly elliptic, 2–14 × 1.5–6 cm, base cuneate, margin dentate or slightly crenate, apex acute with a 0.5–2 cm long tip; petioles 0.5–1.5 cm long; petiolar sheaths 1–2.5 × 0.4–0.7 cm, pubescent, scabrous to the touch, sometimes glabrous, persistent. Staminate inflorescences comprised of 1–2 terminal or axillary spikes 1–5 cm long; anthers 0.9–2 × 0.5–1 mm. Pistillate inflorescences axillary or terminal racemes comprised of 2–8 cymules, each cymule 2–6-flowered; flowers trigonous, 3–4 × 1.5–2.5 mm. Mature fruit globose, fleshy, white.

At present, endemic to Venezuela where it is known only from collections made in Guaramacal National Park (Trujillo; Map 10). Found in cloud forest on both slopes of Guaramacal; 1,600–2,400 m.

***Hedyosmum racemosum*** (Ruiz & Pav.) G. Don, Gen. Hist. 3: 434. 1834. *Tafalla racemosa* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 271. 1798.

FIGURE 2H

*Hedyosmum glabratum* Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 7: 127. 1824; ibid. [qu.] 7: 165. 1824; Ortega et al., BioLlania 5: 36. 1987; Bono, Fl. Veg. Táchira 458. 1996.

Dioecious trees or shrubs, 2–8 m tall; young stems quadrangular in cross-section, older stems terete. Leaves obovate or elliptic, 5–15 × 1.5–6 cm, base cuneate, margin sharply serrate, apex acuminate with a 0.5–1.5 cm long tip, glabrous; petioles 1–2 cm long; petiolar sheaths 1–2.5 cm long, inflated, smooth or with 2 raised ciliate lines extending down from free portion of petioles, persistent, each distal margin with 2 linear to slightly fimbriate stipular appendages 1–2 mm long. Staminate inflorescences spicate, 1–3 spikes per node, 4–9 cm long, sessile or on short peduncles 1–4 mm long; anthers 1–1.5 × 0.5–1 mm, green. Pistillate inflorescences axillary or terminal, racemes or panicles, 2.5–12.5 cm long, comprised of 5–30 cymules, each cymule 2–8-flowered; flowers slightly trigonous, 3–5 × 1.5–3 mm. Mature fruit globose, 0.6–1.2 cm in diameter, fleshy, white.

Restricted to Andean South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, found in the Andes (Barinas, Mérida, Táchira, and Trujillo) and in the Sierra de Perijá (Zulia; Map 11). In the park, found on both slopes including cloud forest between Cerro El Diablo and Qda. Honda; 2,100–2,900 m.

After publishing a revision of the genus *Hedyosmum*, Todzia (1993a) recircumscribed this species by separating elements found in the tepuis of the Venezuelan Guayana from those found in the Andes. Material from Venezuela, Guyana, and Brazil was described as *H. tepuiense* Todzia and differs from *H. racemosum* by its extremely long stipular appendages (4 mm versus 1–2 mm long) and verrucose (versus glabrous) petiolar sheaths.

***Hedyosmum translucidum*** Cuatrec., Caldasia 3: 436. 1945.

Dioecious trees or shrubs, (1–)3–10 m tall; aromatic with citrus-like odor; young stems quadrangular in cross-section, older

**MAP 10.** Distribution of *Hedyosmum guaramacalense*.

**MAP 11.** Distribution of *Hedyosmum racemosum*.

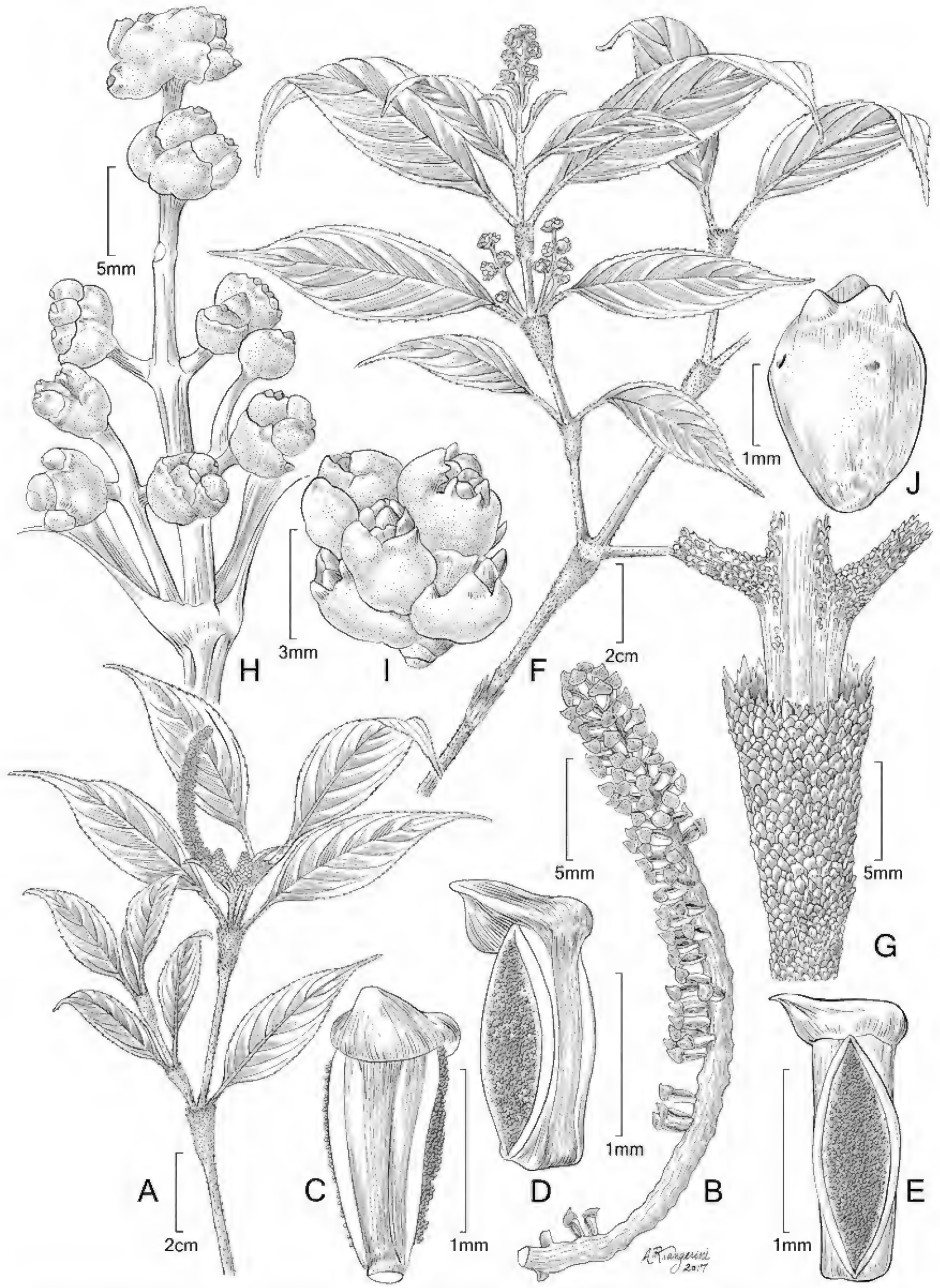



**FIGURE 3.** Chloranthaceae, *Hedyosmum guaramacalense* S. M. Niño & Dorr. **A.** Branch with staminate inflorescences. **B.** Staminate inflorescence. **C–E.** Stamens with acute connectives. **F.** Branch with pistillate inflorescences. **G.** Pubescent petiolar sheath. **H.** Pistillate inflorescence. **I.** Pistillate cyme. **J.** Pistillate flower with 2 pores. (Illustrator A. R. Tangerini; A–E, *Licata et al. 684*; F–J, *Licata et al. 685*).

stems terete. Leaves oblong or elliptic, 5–14.5 × 2–5.5 cm, base cuneate, margin sharply serrate, apex acuminate with a 0.5–1 cm long tip, glabrous; petioles 0.5–1.5 cm long; petiolar sheaths 0.5–2 cm long, smooth or scaly, glabrous, with or without 2 raised, longitudinal lines extending down length of sheath, persistent, stipular appendages lacking. Staminate inflorescences terminal or axillary, 1–3 opposite pairs of spikes, 2.5–12.5 cm long; anthers 1–1.5 × 0.5 mm. Pistillate inflorescences axillary or terminal, simple or branched racemes, 3.5–5 cm long, comprised of 5–12 cymules, each cymule 4–7-flowered; flowers trigonous, 2–2.5 × 0.8–1 mm. Mature fruit globose, 0.9–1.3 cm in diameter, fleshy, white.

Restricted to Andean South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, found only in the Andes (Táchira and Trujillo; Map 12). In the park, found in cloud forest on both slopes of Guaramacal and on the Fila de Agua Fría; 1,900–2,800 m.

*Species excluded from the flora*

*Hedyosmum brasiliense* Miq. does not occur in the the flora of Guaramacal even though Bono (2010: 259) cited a collection (*Steyermark & Rabe 97373*) made at 1,800 m between Boconó and Batatal, which almost certainly was gathered within or adjacent to the boundaries of the park. In fact, *H. brasiliense* is not known to occur in Venezuela (Todzia, 1988) and the name almost certainly is misapplied to one of the five white-fruited species that are found in the park.

**MAP 12.** Distribution of *Hedyosmum translucidum*.

## Lauraceae

S. MIGUEL NIÑO AND L. J. DORR

Trees, shrubs, or herbaceous parasitic vines (not our species); often aromatic. Leaves simple, alternate, rarely whorled, pseudo-opposite, or opposite; leaf blades entire or rarely lobed; commonly with translucent glandular dots; domatia present or not; venation brochidodromous to eucamptodromous, sometimes acrodromous. Inflorescences axillary, usually cymose, paniculate, or umbellate. Flowers actinomorphic, bisexual or unisexual (plants sometimes functionally unisexual, dioecious, or gynodioecious), usually (2)3(4)-merous; hypanthium well developed and fleshy (resembling a calyx tube); perianth of (4)6(9) tepals, 2(3)-seriate, sepaloid, equal or unequal; stamens 9 in whorls of 3 (whorls I–III), 1 or more whorls staminodial (whorl IV) or absent; stamens of whorl III usually with a pair of basal glands; anthers 2- or 4-locular, introrse or extrorse, dehiscence valvate; ovary superior, 1-locular, frequently enclosed in the receptacle; style short; stigma 1, sometimes 2–3-lobed; placentation apical, 1-ovulate. Fruit a drupe or berry, almost always accompanied by the receptacle with 1 seed; endosperm absent.

Lauraceae occur in temperate, subtropical, and tropical regions worldwide but are much more diverse in the tropics. Found in North America (USA), Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Chile, Paraguay, Argentina, and Uruguay), Africa, Madagascar, Asia, Australia, and the Pacific Islands. The greatest diversity of taxa is in the Neotropics and in Asia. Altogether there are ~50 genera and ~2,500–3,500 species of which ~17 genera and ~211 species (43 endemic) are found in Venezuela.

References. Wood (1958); Bernardi (1962); Rohwer et al. (1991); van der Werff (1991); Rohwer (1993a); van der Werff and Richter (1996); Chanderbali et al. (2001); Song et al. (2020).

The circumscription of many genera in the Lauraceae is unsettled and the delimitation of some of the genera treated here is certain to change. Reconciling morphological and molecular data often is difficult; clades defined by molecular data often lack clear-cut or obvious morphological characters. Traditional morphologically defined genera often were based on single character differences in the androecium that are not supported in molecular analyses. In addition to these taxonomic impediments, much of the material underlining our treatment of the family is sterile. Tree taxa especially often were discovered as part of plot studies and sporadic or infrequent flowering has made collecting corresponding fertile material a challenge.

Most of the genera of Lauraceae found in Guaramacal belong to the *Ocotea* complex sensu Chanderbali et al. (2001) or the *Aniba* and *Ocotea* subgroups sensu Rohwer (1993a). These include *Aiouea* Aubl., *Aniba* Aubl., *Endlicheria* Nees, *Nectandra* Rol. ex Rottb., *Ocotea* Aubl., and *Pleurothyrium* Nees. In addition, *Andea* van der Werff and *Damburneya* Raf., which are recognized here, are more recent segregates of *Ocotea* and *Nectandra*, respectively (Trofimov et al., 2016; van der Werff, 2022). As now circumscribed, *Andea*, *Damburneya*, *Nectandra*, and *Pleurothyrium* appear to be monophyletic while *Aiouea*, *Aniba*, and *Ocotea* are polyphyletic and their circumscriptions are likely to change (Rohde et al., 2017; Trofimov et al., 2019; Trofimov and Rohwer, 2020; Penagos Zuluaga et al., 2021). *Beilschmiedia* Nees and *Persea* Mill., which are not part of

the *Ocotea* complex or the *Aniba* and *Ocotea* subgroups, also do not appear to be monophyletic as currently circumscribed (Rohwer, 1993a; Rohwer et al., 2009; Li et al., 2011; Song et al., 2020).

Descriptions of Lauraceae often number the staminal whorls with Roman numerals (I, II, III, IV), starting with the outermost whorl. Whorl III usually has nectaries and the innermost whorl, whorl IV, when present, is staminodial.

## KEY TO THE GENERA OF LAURACEAE

1a. Outer 6 stamens (whorls I and II) 2-locular . . . . . 2
2a. Flowers unisexual (plants usually dioecious). . . . . *Endlicheria*
2b. Flowers bisexual (rarely polygamous). . . . . 3
3a. Staminodes of whorl IV minute to absent . . . . . *Aniba*
3b. Staminodes of whorl IV conspicuous . . . . . 4
4a. Flowers pubescent; tepals ± equal to floral tube. . . . . *Beilschmiedia*
4b. Flowers glabrous; tepals shorter than floral tube. . . . . *Aiouea*
1b. Outer 6 stamens (whorls I and II) 4-locular . . . . . 5
5a. Tepals unequal, the external ones 2/3 or less the size of the inner ones . . . . . *Persea*
5b. Tepals equal or subequal. . . . . 6
6a. Flowers pistillate and hermaphroditic (plants gynodioecious) . . . . . *Andea*
6b. Flowers hermaphroditic . . . . . 7
7a. Outer 6 stamens (whorls I and II) with the lower pair of locules lateral and the other pair introrse; filaments ± equal to anthers . . . . . *Pleurothyrium*
7b. Outer 6 stamens (whorls I and II) with all locules introrse or if 1 pair seemingly lateral, then filaments several times longer than anthers . . . . . 8
8a. Anther locules arranged in an arc; anthers papillate. . . . . 9
9a. Inner surface of tepals papillose throughout or glabrous at the base and only papillose apically; filaments of stamens and staminodes glabrous. . . . . *Nectandra*
9b. Inner surface of tepals pubescent basally and (usually strongly) papillose apically; filaments of stamens and staminodes pubescent . . . . . *Damburneya*
8b. Anther locules arranged in two horizontal rows; anthers not papillate. . . . . 10
10a. Staminodes (whorl IV) absent to conspicuous (in bisexual species only), never sagittate. . . *Ocotea*
10b. Staminodes (whorl IV) conspicuous, sagittate. . . . . *Persea*

## KEY TO STERILE SPECIMENS OF LAURACEAE

1a. Subpáramo and páramo plants; (1,950–)2,350–3,100 m elevation. . . . . 2
2a. Leaf blades glabrous below; apices of young branches glabrous or if pubescent not ferruginous-tomentose . . . . . *Persea mutisii*
2b. Leaf blades whitish or ferruginous below; apices of young branches ferruginous-tomentose . . . . . 3
3a. Leaves petiolate, petioles 0.5–1.4 cm long; blades ovate to elliptic, 4–12 cm long. . . . . *Persea ferruginea*
3b. Leaves sessile; blades elliptic, 10–15(–20) cm long . . . . . *Andea velutina*
1b. Forest plants; 1,500–2,750 m elevation . . . . . 4
4a. Leaves sessile or with petioles 1–3 mm long (rarely longer). . . . . 5
5a. Leaves below shiny or golden-sericeous. . . . . *Andea micans*
5b. Leaves below never shiny or golden-sericeous . . . . . 6
6a. Leaf blades 10–15 cm wide; prophylls glabrous. . . . . *Andea* **sp. A**
6b. Leaf blades 5–7.5(–11) cm wide; prophylls appressed pubescent . . . . . *Andea nidiae*
4b. Leaves with petioles ≥ 3 mm long . . . . . 7
7a. At least some leaf blades ≥ 20 cm long . . . . . 8
8a. Leaves with 12–30 secondary veins on each side of the midrib . . . . . 9
9a. Young branches ferruginous-pubescent; leaves elliptic to elliptic-lanceolate; petioles sheathing; apex of leaf blade with a 1–3.5 cm long tip . . . . . *Pleurothyrium costanense*
9b. Young branches glabrous; leaves obovate or ovate to orbicular; petioles flat, sometimes winged; apex of leaf blade with a 0.3–1.2 cm long tip . . . . . 10
10a. Leaf blades ovate to orbicular, 10–15 cm wide, 12–16 secondary veins on each side of the of the midrib. . . . . *Ocotea* **sp. D**

10b. Leaf blades elliptic, obovate, or oblanceolate, 5–7.5(–11) cm wide, 20–30 secondary veins on each side of the midrib . . . . . *Andea nidiae*
8b. Leaves with 5–12 secondary veins on each side of the midrib . . . . . 11
11a. Petioles terete or flattened . . . . . 12
12a. Terminal branches winged, angular in cross-section; buds elongated or new growth 2–3.5 cm long, tomentose (bright whitish in color) . . . . . *Ocotea* **sp. B**
12b. Terminal branches not winged, terete or angular in cross-section; buds or new growth 0.5–1.5 cm long, ferruginous or whitish tomentose . . . . . 13
13a. Terminal and axillary buds glabrous; veins of leaf blades below glabrous, 8–10(–11) secondary veins on each side of the midrib . . . . . *Persea rigens*
13b. Terminal and axillary buds pubescent or densely appressed pubescent; midrib and secondary veins of leaf blades below with scattered pubesence, 5–8 secondary veins on each side of the midrib . . . . . 14
14a. Terminal buds ferruginous tomentose . . . . . *Ocotea terciopelo*
14b. Terminal buds not ferruginous tomentose . . . . . 15
15a. Stems and leaves drying light brown or yellowish; midrib and secondary veins impressed above, tertiary veins flush or not visible . . . . . *Nectandra* **sp. B**
15b. Stems and leaves drying black or dark brown; midrib slighty raised above and below, secondary and teritary veins always raised below . . . . . *Ocotea puberula*
11b. Petioles channeled (caniculate) or sheathing . . . . . 16
16a. Leaf blades 5–17 cm wide . . . . . *Damburneya purpurea*
16b. Leaf blades 6–9 cm wide . . . . . 17
17a. Young branches densely appressed pubescent, ferruginous when dry; terminal and axillary buds ferruginous . . . . . *Ocotea leucoxylon*
17b. Young branches glabrous; terminal and axillary buds whitish pubescent . . . . . *Aiouea dubia*
7b. Leaf blades mostly ≤ 20 cm long . . . . . 18
18a. Petioles terete, flat, or open (not sheathing) . . . . . 19
19a. Terminal branches densely pubescent; petioles tomentose-ferruginous or densely pubescent . . . . . 20
20a. Petioles 10–25 mm long; leaves below tomentose-ferruginous only on the principal veins; terminal branches striate . . . . . *Nectandra laurel*
20b. Petioles 4–12 mm long; leaves below densely pubescent or tomentose-ferruginous; terminal branches smooth or striate . . . . . 21
21a. Petioles 5–12 mm long; leaf blades 9–15 cm long, apex obtuse to acute or acuminate with a short tip 10–25 mm long; 2–5 secondary veins on each side of midrib *Endlicheria paniculata*
21b. Petioles 4–6 mm long; leaf blades 3.5–7.5 cm long, apex obtuse or with a short tip 4–6 mm long; 7–9 secondary veins on each side of midrib . . . . . *Ocotea guaramacalensis*
19b. Terminal branches glabrous; petioles glabrous . . . . . 22
22a. Undersurface of leaf whitish-glaucous; leaf blades ovate to broadly elliptic-obovate, apex rounded or sometimes acuminate, apical tip 2–4 mm long . . . . . *Beilschmiedia tovarensis*
22b. Undersurface of leaf green (when living); leaf blades elliptic or elliptic-obovate, apical tip 5–12 mm long . . . . . 23
23a. Midrib and secondary veins impressed above; 6–12 secondary veins on each side of the midrib; petioles 3–10 mm long . . . . . *Nectandra* **sp. A**
23b. Secondary and tertiary veins raised above; 4–10 secondary veins on each side of the midrib; petioles 4–20 mm long . . . . . 24
24a. Fresh stems and leaves with a disagreable odor when broken or crushed; terminal branches terete and solid; leaf blades without minute black dots; domatia present in axils of midrib and secondary veins below . . . . . *Ocotea* **sp. E**
24b. Fresh stems and leaves without a disagreable odor when broken or crushed; terminal branches terete or somewhar angular in cross-section; leaf blades with minute black (glandular?) dots above and below; domatia absent . . . . . *Ocotea puberula*
18b. Petioles deeply channeled (caniculate) or sheathing . . . . . 25
25a. Terminal branches densely ferruginous-tomentose; fresh stems and leaves with a cinnamon-like odor when broken or crushed . . . . . *Aniba cinnamomiflora*

25b. Terminal branches smooth or scattered pubescent, not ferruginous-tomentose; fresh stems and leaves without a cinnamon-like odor when broken or crushed . . . . . 26
26a. Leaf blades ovate, ovate-elliptic, or ovate-oblong, base obtuse, rounded to cordate . . . . . 27
27a. Petioles 1–2 cm long; leaf blade apex sharply acuminate or acute; 8–12 secondary veins each side of the midrib . . . . . *Ocotea vaginans*
27b. Petioles 1.5–6 cm long; leaf blade apex acute or rounded; (12–)14–16 secondary veins on each side of the midrib . . . . . *Persea caerulea*
26b. Leaf blades elliptic, base acute, attenuate, or acuminate . . . . . 28
28a. Terminal branches terete, striate, glabrous; leaf blades with 10–14 secondary veins on each side of the midrib . . . . . ***Persea* sp. A**
28b. Terminal branches terete or rectangular, smooth or striate, glabrous or pubescent; leaf blades with 6–11 secondary veins on each side of the midrib . . . . . 29
29a. Leaf blades with 6–9 secondary veins on each side of the midrib; axillary buds absent . . . . . *Ocotea floribunda*
29b. Leaf blades with 8–11 secondary veins on each side of the midrib; axillary buds densely pubescent . . . . . *Persea meridensis*

## *Aiouea* Aubl.

*Aiouea* Aubl., Hist. Pl. Guiane 1: 310. 1775.
*Mocinnodaphne* Lorea-Hern., Acta Bot. Mex. 32: 26. 1995.

Trees or rarely shrubs, sometimes with xylopodia. Leaves alternate, evergreen (rarely deciduous), penninerved (rarely triplinerved), glabrous above, glabrous or rarely pubescent below; domatia often present in the axils of veins. Inflorescences thyrsopaniculate, distributed the length of the branches (subterminal) or in leaf axils. Flowers bisexual (rarely polygamous?), small, pedicellate, bracts caducous; floral tube cylindrical or campanulate, longer than or rarely as long as the perianth; tepals 6, erect, equal; tube and tepal bases pilose within; androecial whorls 4; fertile stamens 9, occasionally 6 or 3; whorl I fertile, whorls II and III staminodial or not, introrse, extrorse, or latrorse, stamens of whorl III with enlarged sessile glands, staminodes of whorl IV stipitiform, triangular or clavate; filaments narrower than anthers; anthers 2- (our species) or 4-locular; ovary ovoid or globose, glabrous, immersed in the floral tube; style cylindrical, widening toward the stigma; stigma discoidal. Fruit an ellipsoid or subglobose 1-seeded berry borne on a swollen pedicel that merges with a shallow cupule; tepals persistent or less often deciduous.

A Neotropical genus found in Mexico, Central America, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, and Paraguay); approximately 70–75 species of which ~8 occur in Venezuela.

References. Kubitzki and Renner (1982); Rohde et al. (2017).

Chanderbali et al. (2001) noted that the few species of *Aiouea* they examined in a molecular study of Lauraceae were nested among Neotropical species of *Cinnamomum* Schaeff. With expanded sampling, Rohde et al. (2017) showed that the Neotropical and Paleotropical species of *Cinnamomum* do not form a monophyletic group. Instead, the American species of *Cinnamomum* form a clade within which most species of the Neotropical genus *Aiouea* are nested. Consequently, Rohde et al. (2017) decided to expand *Aiouea*, which is the oldest generic name that can be applied to this clade. Previously, *Aiouea* was separated from Neotropical *Cinnamomum* by the number of locules per anther (2 versus 4), but this character is known to be variable within several other lauraceous genera. The *Aiouea*/Neotropical *Cinnamomum* clade of Rohde et al. (2017) is sister to the predominantly Neotropical *Ocotea* complex.

Van der Werff (2019) disagreed with the circumscription of *Aiouea* proposed by Rohde et al. (2017) and without elaboration chose to exclude species with 4-locular anthers from *Aiouea* and retain them in *Cinnamomum*. Although this would make the morphological circumscription of *Aiouea* simpler, it does not resolve the paraphyly of *Cinnamomum*.

***Aiouea dubia*** (Kunth) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 34. 1889; Huérfano et al., Libro Rojo Fl. Venez., ed. 2, 276. 2020. *Cryptocarya dubia* Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 2: 133. 1817; ibid. [qu.] 2: 167. 1817.

Trees, 6–14 m tall; young branches striate, terete, glabrous; bracts (prophylls) usually present, pyramidal, 3–6 mm long; terminal buds grayish-whitish appressed pubescent. Leaves elliptic or narrowly elliptic, 5–22 × 4–9 cm, base acute, margin undulate, apex acuminate, midrib impressed above, (5–)8–12 secondary veins each side of the midrib, glabrous, midrib prominent below, glabrous or rarely with a few hairs on midrib, coriaceous; petioles decurrent or sheathing, 0.7–1.6 cm long, canaliculate, glabrous. Flowers ~2.5–3.5 mm long, glabrous, floral tube obconical to campanulate, pilose within (sometimes pilose only at base); tepals shorter than floral tube; fertile stamens in 3 whorls (I–III); staminodes in whorl IV; outer 6 stamens introrse, stamens of whorl III extrorse with glands; ovary globose; style ± equal to ovary in length; stigma as thick or thicker than style in cross-section. Fruit unknown.

Andean South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, known only from the Andes (Mérida and Trujillo; Map 13). In the park, found in cloud forest on the north slope of Guaramacal; 1,950–2,500 m.

MAP 13. Distribution of *Aiouea dubia*.

We are not completely confident that this is the correct name for our taxon because all the material known from the park is sterile (see Dorr et al., 2000). Among the Lauraceae known from Guaramacal, *Aiouea dubia* is distinctive in being entirely glabrous with the midrib impressed above and raised below, and with the leaf base decurrent on the apex of the petiole. The description of the flowers presented here is taken from Kubitzki and Renner (1982).

*Aiouea truxillensis* Kosterm. was placed in synonymy under *A. dubia* by van der Werff (2008), even though the former long had been considered a doubtful species (Bernardi, 1962; Kubitzki and Renner, 1982). *Aiouea truxillensis* differs from our material in the size and shape of the leaf blades, and in having conspicuous domatia in the axils of the lateral veins below.

## *Andea* van der Werff

*Andea* van der Werff, Ann. Missouri Bot. Gard. 107: 428. 2022.

Gynodioecious trees or shrubs; twigs stout, terete, solid. Leaves alternate, sessile or nearly sessile, pinnately veined; domatia absent. Inflorescences paniculate-cymose, borne in the axils of leaves or rarely borne in the axils of bracts, sometimes reduced and appearing racemose. Flowers pistillate or hermaphroditic, large; tepals 6, equal, rotate at anthesis. Pistillate flowers: staminodes 9, inner 3 with 2 glands at their base, staminodes (whorl IV) lacking; pistil well-developed; stigma conspicuous and raised above the level of the staminodes. Hermaphroditic flowers: stamens 9, stout; ovary swollen; stigma conspicuous; pistil equal to or slightly shorter than stamens; staminodes (whorl IV) usually absent. Cupule present, shallowly bowl-shaped, margin entire, simple; fruit ellipsoid; tepals not persisting, deciduous.

A Neotropical genus of 25 species found in Central America (Costa Rica) and Andean South America (Colombia, Venezuela, Ecuador, and Peru). Four species occur in Venezuela.

The genus *Andea* includes all species formerly placed in the *Ocotea smithiana* group (van der Werff, 2017, 2020, 2022), which in the phylogenetic analysis of Penagos Zuluaga et al. (2021, fig. 2 sub Pluriocotea) resolves as a well-supported clade. Morphologically *Andea* is united by the presence of pistillate and hermaphroditic flowers (gynodioecy), "thick" twigs, (sub)sessile leaves, and relatively large, rotate flowers.

### KEY TO THE SPECIES OF *ANDEA*

1a. Leaf blades below densely sericeous, golden-sericeous, or ferruginous pubescent . . . . . 2
2a. Leaf blades below almost always with a golden-sericeous indumentum of appressed minute hairs < 0.2 mm long; leaf blades above with similar appressed minute hairs on secondary veins . . . . . ***A. micans***
2b. Leaf blades below densely ferruginous-tomentose especially toward base and on midrib with hairs 0.2–1 mm long; leaf blades above moderately ferruginous-tomentose toward the base . . . . . ***A. velutina***
1b. Leaf blades below glabrous or with scattered pubescence on veins only . . . . . 3
3a. Leaf blades obovate or oblanceolate, 5–7.5(–11) cm wide; terminal buds appressed pubescent . . . . . ***A. nidiae***
3b. Leaf blades elliptic to narrowly ovate, 10–15 cm wide; terminal buds glabrous . . . . . **A. sp. A**

***Andea micans*** (Mez) van der Werff, Ann. Missouri Bot. Gard. 107: 429. 2022. *Ocotea micans* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 297. 1889.

*Ocotea sericea* auct., non Kunth; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 319. 2010.

Trees, 9(–25) m tall; twigs angular in cross-section, densely tomentellous; terminal buds densely appressed pubescent. Leaves elliptic to narrowly elliptic, 15–25 × 4–6.5(–7) cm, base acute, margin revolute only near the base, apex acuminate, secondary veins 15–20 on each side of the midrib, glabrous and bright green above with midrib impressed and secondary veins slightly raised, shiny- or golden-sericeous below with veins scarcely visible, chartaceous or coriaceous; sessile or shortly petiolate, petioles 1–2(–10) mm long. Inflorescences borne in axils of leaves, 5–10(–17) cm long with dispersed indumentum. Pistillate flowers: tepals spreading or reflexed, outer surface densely pubescent, inner surface sparsely pubescent to subglabrous; staminodes ~1 mm tall, glands at base of inner stamens; pistil ~3 mm tall. Hermaphroditic flowers: not observed. Cupule cup-shaped; fruit ~2.2 × 1.3 cm, almost black when mature.

Restricted to northern Andean South America (Colombia and Venezuela). In Venezuela, found in the Andes (Mérida and Trujillo) and in the Cordillera de la Costa (Aragua; Map 14). In the park, found in cloud forest on the south slope of Guaramacal near Cerro El Diablo and Qda. Honda, and at the edge of páramo on the north slope of Guaramacal; 2,300–2,350 m.

*Andea micans* is a poorly known species originally described from and thought to be restricted to Colombia (van der Werff, 2020). The material from Guaramacal is sterile and referred to this species with some reservation; the flower and fruit descriptions above were taken from van der Werff (2017). *Andea micans* could be confused with *A. velutina* (Meisn.) van der Werff, but the former has bright golden-sericeous indumentum on the leaves below, 15–20 secondary veins each side of the midrib, and very short (0.5 mm long) appressed hairs while the latter has densely tomentose-ferruginous indumentum on the leaves below, 10–12 secondary veins each side of the midrib, and long (1–2 mm long) hairs.

*Andea micans* also could be confused with *A. sericea* (Kunth) van der Werff, but the terminal buds and lower leaf surfaces of the latter species are silky pubescent (i.e., sericeous), and the leaves are closely spaced and often overlapping. In addition, *A. sericea* is restricted to Colombia and Ecuador (van der Werff, 2019, 2020) where it is found at ~3,000 m.

Van der Werff (2017, 2020) relying on morphology included *Ocotea micans* (≡ *Andea micans*) in the *Ocotea smithiana* group, which he (van der Werff, 2022) subsequently recognized as the genus *Andea*. Panagos Zuluaga et al. (2021) relying on molecular data included *O. micans* in a clade with *O. caesariata* van der Werff (≡ *A. velutina*) and other members of the *Ocotea smithiana* group. Previous molecular studies (Trofimov et al., 2019; Trofimov and Rohwer, 2020), however, either placed *O. micans* in a clade with *O. minarum* Nees & Mart. (see van der Werff, 2022) or found it to be isolated and sister to the *Ocotea insularis* group.

***Andea nidiae*** (van der Werff) van der Werff, Ann. Missouri Bot. Gard. 197: 429. 2022. *Ocotea nidiae* van der Werff, Novon 28: 219, fig. 10. 2020.

*Ocotea karsteniana* auct., non Mez; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001].

Trees, 4–12(–20) m tall; twigs angular in cross-section, glabrous, lenticellate or not; terminal buds appressed pubescent. Leaves obovate or oblanceolate, 20–30 × 5–7.5(–11) cm, base cuneate or attenuate, margin entire but base sometimes revolute, apex variable in leaves from the same branch, acuminate, obtuse, or more frequently acute, glabrous above and below, 20–30 secondary veins each side of the midrib, only the midrib prominent below, chartaceous; sessile or subsessile, petioles 1–3 mm long. Inflorescences tomentose. Hermaphroditic flowers ("staminate" in original description): tepals spreading or reflexed, outer and inner surfaces moderately pubescent, more densely so at base of inner surface, glands at base of inner stamens; pistil ~3 mm tall. Cupule flattened; fruit 10–15 × 7–9 mm.

Endemic to Venezuela where it is restricted to the Andes (Lara, Mérida, and Trujillo; Map 15). The type locality is Cerro Cerrón, which is part of the disputed area between Lara and Falcón states (mapped here as Lara). In the park, found on the north slope of Guaramacal on the trail from the Laguna de Aguas Negras to Agua Fría; 2,100–2,500 m.

Our material differs in a number of respects from the type of *Andea nidiae*. In particular, the terminal buds are appressed pubescent (versus glabrous), the leaves are narrower, and there are more secondary veins on each side of the midrib (20–30 versus 8–12).

***Andea velutina*** (Meisn.) van der Werff, Ann. Missouri Bot. Gard. 107: 430. 2022. *Pleurothyrium velutinum* Meisn., in de Candolle, Prodr. 15(1): 170. 1864. *Ocotea calophylla* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 295. 1839, nom. illeg.

**MAP 14.** Distribution of *Andea micans*.

**MAP 15.** Distribution of *Andea nidiae*.

superfl.; Bono, Fl. Veg. Táchira 595. 1996; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 318. 2010. *Ocotea caesariata* van der Werff, Novon 25: 354. 2017, nom. nov.

Trees, 9(–20) m tall; twigs angular in cross-section, densely tomentose, hairs 1–2 mm long, ferruginous; terminal buds densely ferruginous pubescent. Leaves elliptic, 10–15(–20) × 4–8 cm, base acute, margin weakly or strongly revolute near base, apex acute or acuminate with 1–6 mm long tips, 10–12 secondary veins each side of the midrib, secondary veins raised and scarcely visible below, impressed or sunken above, moderately tomentose-ferruginous above especially toward base, densely tomentose-ferruginous below especially toward base and on midrib, coriaceous; sessile. Inflorescences borne in axils of leaves, 8–12(–25) cm long, densely ferruginous-tomentose. Hermaphroditic flowers ("staminate" in van der Werff, 2017): ~6–8 mm in diameter, tepals spreading, outer surface densely pubescent, inner surface glabrous or sparingly pubescent at margin, stamens 9, glabrous, all 4-locular, glands present at base of inner stamens; pistil ~3 mm tall. Pistillate flowers: ~8 mm in diameter, tepals spreading, outer surface densely pubescent, inner surface pubescent; pistil ~3 mm tall. Cupule bowl-shaped; fruit ellipsoid, ~10–15 × 7–9 mm.

Found in Andean South America (Colombia, Venezuela, and Ecuador). In Venezuela, collected in the Andes (Lara, Mérida, Táchira, and Trujillo) and in the Cordillera de la Costa (Anzoátegui and Monagas; Map 16). The sole park record is from the upper limit of cloud forest on the south slope of Guaramacal; 2,550 m.

### *Andea* sp. A

*Ocotea smithiana* auct., non O. C. Schmidt; Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001].

Trees, 8 m tall; terminal branchlets angular in cross-section; terminal buds glabrous. Leaves elliptic to narrowly ovate, 20–35 × 10–15 cm, base cuneate, sometimes auriculate, margin entire to slightly undulate, apex rounded or acute, sometimes acuminate, 18–25 secondary veins each side of the midrib, midrib impressed and secondary veins slightly raised above, veins raised below, glabrous or the secondary veins below with dispersed pubescence, coriaceous; petioles 1–3 mm long, flattened, reddish or leaves almost sessile. Inflorescences, flowers, and fruit unknown.

At present, known only from collections made in Guaramacal National Park in Venezuela (Trujillo; Map 17). In the park, found in cloud forest at lower elevations on both slopes of Guaramacal; 1,850–1,950 m.

All the vouchers (*Cuello et al. 1197*, *1307*, *1707*) for the presence of this species in Guaramacal are sterile and none have been matched to any species of *Andea* nor to the Andean species of *Ocotea* listed by van der Werff (2020). The large leaves of *Andea* sp. A are similar to those of *A. lorda* (van der Werff) van der Werff, described from and apparently restricted to Antioquia, Colombia. Their leaf bases, however, are very different, flat in the former versus strongly revolute in the latter. *Andea* sp. A also appears similar to *A. hueckii* (Bernardi) van der Werff, described from Mérida state. Like *A. hueckii* the leaf bases of *Andea* sp. A are truncate, the leaves are chartaceous (representing a flush of young leaves?) versus coriaceous, and shortly petiolate versus sessile. Rohwer (1986) considered *A. hueckii* (as *O. hueckii* Bernardi) to be a synonym of *A. smithiana* (O. C. Schmidt) van der Werff (as *O. smithiana* O. C. Schmidt) while van der Werff (2008, 2020, 2022) accepted both species and restricted the former to Venezuela and the latter to Colombia.

## *Aniba* Aubl.

*Aniba* Aubl., Hist. Pl. Guiane 1: 327. 1775.

Trees or rarely shrubs; sometimes with xylopodia. Leaves alternate, uniformly distributed or sometimes crowded at the ends

**MAP 16.** Distribution of *Andea velutina*.

**MAP 17.** Distribution of *Andea* sp. A.

of branches, evergreen, penninerved, ± glabrous above, pubescent or sometimes minutely papillose below; domatia absent. Inflorescences thyrso-paniculate, congested, rarely elongated, in the axils of bracts and/or leaves; bracts caducous. Flowers bisexual (hermaphroditic), small, pedicellate; bracts caducous; floral tube conspicuous, ± urceolate; tepals 6, erect, equal or the exterior ones smaller than the internal ones; fertile stamens usually 9(6); filaments as wide or wider than anthers; anthers 2-locular; outer 6 stamens strictly introrse or sublateral-introrse; inner 3 stamens erect, each with 2 glands at base, extrorse or extrorse-latrorse; whorl III sometimes staminodial; ovary ellipsoid or ovoid, glabrous or pilose, included within the floral tube; style cylindrical; stigma minute, oblique. Fruit a berry, ellipsoid or subglobose, included in a simple- or rarely double-margined cupule; tepals deciduous.

A Neotropical genus of ~50 species found in Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil). Eighteen species occur in Venezuela.

REFERENCES. Kubitzki and Renner (1982); Penagos Zuluaga et al. (2021).

*Aniba* is part of the *Ocotea* complex of Neotropical lauraceous genera. Although *Aniba* has floral characters that easily distinguish it from other genera in the complex (viz., 2-locular anthers and a deep floral tube), it is not monophyletic (Penagos Zuluaga et al., 2021). Two separate lineages of *Aniba* were recovered by Penagos Zuluaga et al. (2021, fig. 3). The sole species found in Guaramacal is part of a well-supported clade that includes not only the type of the genus but also species of *Licaria* Aubl. The other lineage that contains *Aniba* species is part of a distinct clade that also includes different species of *Licaria* and species of *Ocotea*.

***Aniba cinnamomiflora*** C. K. Allen, Mem. New York Bot. Gard. 10(5): 49, fig. 30. 1964; van der Werff, in Berry et al., Fl. Venez. Guayana 5: 706. 1999; Wingfield and van der Werff, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 530, t. 146a. 2007.

FIGURE 4A,B

Trees, 4–25 m tall; young twigs slightly rusty-tomentellous; terminal buds densely tomentose-ferruginous. Leaves elliptic or lanceolate, 5–15 × 2.5–6 cm, base acute or obtuse, slightly decurrent on petiole, margin revolute, apex acute or acuminate, apical tip to 1 cm long, glabrous above, microscopically pubescent below, 5–9 secondary veins each side of the midrib, midrib, secondary, and tertiary veins impressed above, midrib prominent, secondary veins slightly raised and tertiary veins impressed below, leaves below greenish-yellow when alive but drying yellow or cream, chartaceous to coriaceous; petioles 0.5–2 cm long, canaliculate, indumentum similar to that of young twigs. Inflorescences paniculate, crowded at apex of branches in axils of bracts, densely ferruginous-tomentose, few-flowered. Flowers small, ~3 × 1.8 mm, yellowish- or whitish-green rusty-tomentellous; pedicels 1–2 mm long; tepals subequal, 1–1.4 mm long, external tepals ovate, margins ciliate; stamens included, ~0.8 mm tall, those of whorls I and II with depressed glabrous anthers, slightly protruding connectives, and narrow filaments; anthers of whorl III with truncate glabrous anthers; staminodes minute, stipitiform or absent; pistil ~1.5 mm tall; style massive; stigma truncate, minute. Cupule merging into a thick pedicel; fruit 1.8 × 1.3 cm.

Found in Central America (Costa Rica and Panama) and South America (Venezuela); expected to occur in Colombia. In Venezuela, known from the Andes (Mérida, Portuguesa, Táchira, and Trujillo), the Cordillera de la Costa (Aragua and Miranda), the Venezuelan llanos (Apure), and the Venezuelan Guayana (Amazonas; Map 18). In the park, found in cloud forest on the north slope of Guaramacal; 1,600–2,200 m.

COMMON NAMES. Aceituno, canelo, laurel, laurel canelo.

USES. Dorr et al. (2000) reported that this species is used as an anaesthetic to treat skin sores and that the wood is used for construction.

The wood, leaves, and flowers all have a pleasant odor.

## ***Beilschmiedia*** **Nees**

*Beilschmiedia* Nees, in Wallich, Pl. Asiat. Rar. 2: 61, 69. 1831.

Trees or shrubs. Leaves generally alternate, sometimes opposite or subopposite, leaf blades simple, pinnatinerved; domatia absent. Inflorescences paniculate or racemose, the terminal branches of panicles not strictly cymose. Flowers bisexual (hermaphroditic); tepals 6, generally equal, ovate or elliptic, united at their base, generally deciduous; fertile stamens 9 or 6; filaments generally shorter than anthers; anthers 2-locular, whorls I and II introrse, whorl III extrorse or almost introrse, glands of the 3 innermost staminodes globose; staminodes 3 in whorl IV or absent, or rarely 6, then 3 each in whorls III and IV, staminodes in whorl IV conspicuous, saggitate or deltoid; ovaries with flat receptacles or shallowly cupulate. Fruit a 1-seeded berry, ellipsoidal, spherical, or pyriform; cupule absent; tepals deciduous.

A pantropical genus of ~250–275 species found in Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, Guyana, French Guiana, Ecuador, Peru, Bolivia, Brazil, and Chile), Africa, Madagascar, Asia, and the Pacific Islands. The genus is most diverse in tropical Africa and Asia. Eight species are known from Venezuela.

REFERENCE. Nishida (1999).

Rohwer (1993a) speculated that *Beilschmiedia* might not be monophyletic. Indeed, in Song et al. (2020, fig. 3) *Beilschmiedia* is paraphyletic with species of *Syndiclis* Hook. f. and *Potameia* Thouars embedded within the same clade, and this clade is sister to *Endiandra* R. Br. and *Cryptocarya* R. Br. In a separate analysis in the same paper, Song et al. (2020, fig. 2) recovered a monophyletic *Beilschmiedia* as did Liu et al. (2013). In these two studies, however, the sampling was not extensive and all the species of *Beilschmiedia* examined were Asian.

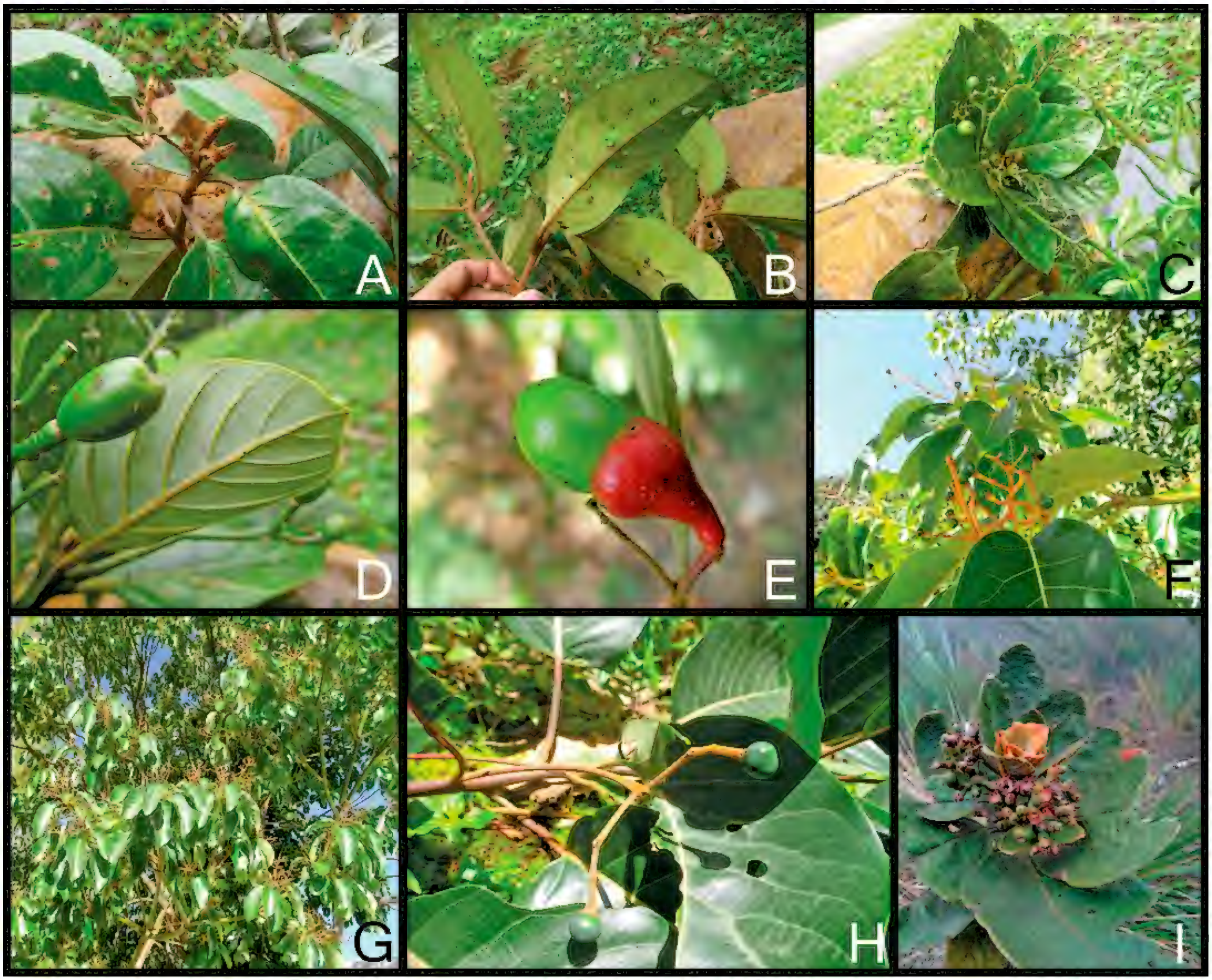



**FIGURE 4. A, B.** Lauraceae, *Aniba cinnamomiflora* C. K. Allen. A. Inflorescence and upper surface of leaf blades. B. Lower surface of leaf blades. **C, D.** *Beilschmiedia tovarensis* (Klotzsch & H. Karst. ex Meisn.) Sach. Nishida. C. Infructescence and upper surface of leaf blades. D. Fruit and lower surface of leaf blade. **E.** *Endlicheria paniculata* (Spreng.) J. F. Macbr. Fruit. **F–H.** *Persea caerulea* (Ruiz & Pav.) Mez. F. Inflorescence. G. Habit. H. Fruits and upper surface of leaf blades. **I.** *P. ferruginea* Kunth. Infructescence and upper surface of leaf blades. (A–I, photographer D. Canelón).

***Beilschmiedia tovarensis*** (Klotzsch & H. Karst. ex Meisn.) Sach. Nishida, Ann. Missouri Bot. Gard. 86: 696. 1999. *Hufelandia tovarensis* Klotzsch & H. Karst. ex Meisn., in de Candolle, Prodr. 15(1): 65. 1864.

FIGURE 4C,D

*Beilschmiedia sulcata* auct., non (Ruiz & Pav.) Kosterm.; Ortega et al., BioLlania 5: 43. 1987.

Trees, (6–)14–20 m tall; buds of new branchlets pubescent with appressed ferruginous hairs. Leaves alternate, ovate to broadly elliptic-obovate, notably variable even on the same branch, 4–9 × 3–7 cm, base cordate or obtuse, sometimes cuneate, margin not inrolled, apex rounded, sometimes acuminate, coriaceous to chartaceous, glabrous above, pubescent with appressed hairs and whitish-glaucous below, secondary veins 5–7(–11) each side of the midrib, prominent above, impressed below; petioles short, 0.5–1.4 cm long. Inflorescences 4–15 cm long; floral pedicels of the lateral divisions 0.5–1.5 mm long, pedicels of the central flowers up to 3 mm long. Flowers 2–3 mm long, pubescent, yellowish-white or

**MAP 18.** Distribution of *Aniba cinnamomiflora*.

greenish-yellow; tepals 6, equal, ovate to elliptic, ± equal to floral tube; stamens 9; anthers 2-locular, apices glabrous; glands of innermost 3 stamens globose; staminodes 3, sagittate; pistil ~1 mm tall; ovary as long as and gradually narrowed into the style. Fruit ovoid, 2.5–3.5 × 1.5–2 cm, purple black.

Central America (Costa Rica and Panama) and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, recorded from the Andes (Mérida, Portuguesa, and Trujillo) and the Cordillera de la Costa (Aragua, Distrito Capital, Monagas, and Yaracuy; Map 19). Found in cloud forest on both slopes of Guaramacal; 1,600–2,350 m.

**MAP 19.** Distribution of *Beilschmiedia tovarensis*.

## ***Damburneya* Raf.**

*Damburneya* Raf., Sylva Tellur. 136. 1838.

Trees or shrubs. Leaves evergreen, alternate, penninerved, tertiary venation ± evenly reticulate to mixed (not scalariform). Flowers bisexual (hermaphroditic); tepals 6, ± equal, inner surface pubescent (sometimes inconspicuously pubescent), outer surface pubescent basally and strongly papillose apically, shed as a ring after anthesis; fertile stamens 9; filaments distinct, pubescent; anthers transverse-elliptic to almost rectangular, apex rounded to truncate, 2- or 4-locular, usually arranged in a shallow arc but sometimes in 2 superposed pairs; staminodes 3, filaments pubescent, glandular headed, the latter usually ± rhomboidal, rarely sagittate; ovary inserted in a shallowly bowl- to cup-shaped receptacle. Fruit almost completely exserted; cupule shallowly bowl-shaped to turbinate.

A New World genus of ~25 species found in North America (USA), Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, French Guiana, Ecuador, Peru, Bolivia, and Brazil); naturalized in Africa. Three species occur in Venezuela.

References. Rohwer (1993b); Trofimov et al. (2016, 2019).

A molecular analysis of *Nectandra* by Trofimov et al. (2016) indicated that the genus as circumscribed by Rohwer (1993b) was polyphyletic. Their molecular study showed strong support for a monophyletic *Nectandra* s. str. sister to *Pleurothyrium* Nees and a more distantly-related monophyletic *N. coriacea* group. Consequently, Trofimov et al. (2016, 2019) transferred the species of the *N. coriacea* group to *Damburneya*, the oldest generic name available. The isolated nature of the *N. coriacea* group had been recognized by Rohwer (1993b) who nonetheless retained the species within *Nectandra* s.l.

Specimens of *Damburneya* can be confused easily with those of *Nectandra* inasmuch as the diagnostic morphological characters separating the two genera are inconspicuous. In *Damburneya* the adaxial side of the tepals bears at least some ± straight hairs at the base, often intergrading with crinkled papillae-like hairs distally, whereas in *Nectandra* s.str the adaxial side of the tepals is usually papillose throughout, or glabrous at the base and only papillose distally. Also, the filaments of stamens and staminodes are almost always pubescent in *Damburneya* while they are glabrous in *Nectandra*. Uniform and reticulate teritary venation is very common in *Damburneya* whereas the majority of *Nectandra* species show scalariform tertiary venation.

***Damburneya purpurea*** (Ruiz & Pav.) Trofimov, Taxon 65: 991. 2016. *Laurus purpurea* Ruiz & Pav., Laurographia t. 351. [1804–]1813. *Nectandra purpurea* (Ruiz & Pav.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 443. 1889; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001]; Wingfield and van der Werff, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 532. 2007; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 318. 2010.

Trees, 5–12 m tall; young branches minutely appressed-puberulent to glabrescent. Leaves elliptic to oblong-elliptic, 10–26 × 5–17 cm, base acute to obtuse or (rarely) subtruncate, apex acuminate, glabrous below with visible hairs in the axils of the principal veins, 6–8 secondary veins each side of the midrib, midrib impressed above, somewhat prominent below; petioles 0.5–3.5 cm long. Inflorescences in the axils of foliage leaves as well as in the axils of bracts (cataphylls), 10–15 cm long. Flowers 3–5 mm in diameter, white or cream; tepals 1–1.2 × 1.5–2.4 mm, ± equal; stamens in 3 whorls; staminodes shorter than stamens; pistil ~1.5 mm tall; ovary subglobose to pyriform. Fruit ellipsoidal, 1.5–2 cm long; cupule shallowly bowl-shaped.

Mexico, Central America, and South America (Colombia, Venezuela, French Guiana, Ecuador, Peru, Bolivia, and Brazil). In Venezuela, recorded from the Andes (Portuguesa and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Falcón), and the Venezuelan llanos (Barinas; Map 20). In the park, found in cloud forest on the south slope of Guaramacal along the Camino Real from Paramito to Batatal; 1,600 m.

COMMON NAME. Laurel aguacatico.

The exact date of publication of *Laurus purpurea* is unknown. The name was included in the fourth volume of the Flora Peruviana et Chilensis, which Ruiz and Pavon completed in 1804 but did not publish. The text of this volume was only validly published more than a century later (Ruiz and Pavon, 1956) while the plates, which include analyses (details of flowers and fruit aiding identification), were long thought to have first been available in 1830 (Stafleu and Cowan, 1983; Rohwer, 1993b) until evidence was discovered that Pavon sent Sir James Smith a set of these plates in July 1813 (see Moraes in Trofimov et al., 2016). We have adopted the title "Laurographia" for these 28 plates (tt. 345–372) to distinguish them from the posthumous publication of the text and identical plates.

**MAP 20.** Distribution of *Damburneya purpurea*.

## *Endlicheria* Nees

*Endlicheria* Nees, Linnaea 8: 37. 1833, nom. cons.

*Rhodostemonodaphne* Rohwer & Kubitzki, Bot. Jahrb. Syst. 107: 135. 1985, syn. nov. *Synandrodaphne* Meisn., in de Candolle, Prodr. 15(1): 176. 1864, non *Synandrodaphne* Gilg, Bot. Jahrb. Syst. 3: 362. 1915, nom. cons.

Usually dioecious trees or shrubs (rarely scandent shrubs), generally fragrant. Leaves alternate or whorled, penni- or rarely triplinerved, chartaceous or coriaceous; domatia rarely present. Inflorescences thyrso-paniculate, generally axillary, many-flowered. Flowers unisexual; lateral flowers in a cyme always strictly opposite; tepals 6 (2 rows of 3), equal, erect, reflexed, or spreading at anthesis. Staminate flowers: fertile stamens 9, whorl III with glands, filaments exceeding anthers or absent; anthers 2- or 4-locular (sometimes both 2- and 4-locular within a flower), whorls I and II introse, whorl III ± extrorse; staminodes lacking; pistillode present (much reduced) or absent. Pistillate flowers: staminodes 9, glands conspicuous; style short, thick; stigma large. Fruit a 1-seeded drupe; cupule shallow, variously shaped, generally smooth and glabrous, margin entire; tepals mostly deciduous.

A Neotropical genus of ~80–100 species found in Central America (Costa Rica and Panama) and South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, Brazil, and Paraguay). Approximately 30 species occur in Venezuela.

REFERENCES. Chanderbali (2004); Madriñán (2004); Penagos Zuluaga et al. (2021).

Phylogenetic data (Chanderbali et al., 2001; Chanderbali, 2004; Penagos Zuluaga et al., 2021) provide convincing evidence for placing *Rhodostemonodaphne* in synonymy under *Endlicheria*, which is the synonymy adopted here. Both *Endlicheria* and *Rhodostemonodaphne* have unisexual flowers and the plants are dioecious. The key morphological character formerly used to differentiate the two genera is the number of anther locules: 2 per anther in *Endlicheria* and 4 in *Rhodostemonodaphne*. Other genera of Lauraceae are known to have both 2- and 4-locular anthers.

***Endlicheria paniculata*** (Spreng.) J. F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2/3): 850. 1938. *Citrosma paniculata* Spreng., Syst. Veg. 2: 545. 1825.

FIGURE 4E

*Cryptocarya hirsuta* Schott, Syst. Veg., ed. 16, 4(2, Cur. Post): 405. 1827. *Endlicheria hirsuta* (Schott) Nees, Linnaea 8: 38. 1833.

*Endlicheria racemosa* Lasser, Bol. Técn. Minist. Agric. no. 3: 8, t. 2. 1942.

Trees, 10–15 m tall; branchlets angular in cross-section, densely ferruginous-tomentose apically, very fragrant when crushed. Leaves elliptic, 9–15 × 3.5–5 cm, base acute to obtuse, margin minutely recurved, apex obtuse to acute or acuminate with a 1–2.5 cm long tip, dark green, smooth and glabrous above, light green to whitish and densely pubescent below, secondary veins 2–5(–6) on each side of the midrib, anastomosing; petioles 5–12 mm long, appressed tomentose. Inflorescences densely pubescent, 3–5 cm long. Staminate

flowers: tepals ovate to ligulate, silvery-gray strigose within, spreading at anthesis; stamens of whorls I and II stipitate; anthers glabrous, 2-locular; stamens of whorl III broadly stipitate. Pistillate flowers: similar to staminate flowers except stamens sterile; ovary glabrous, ovoid; stigma broadly 3-lobed. Cupules 4–5 mm wide (when dry), red, glabrous, rugose, smooth-edged. Fruit a drupe, ovoid, 1–1.5 × 0.4–0.5 cm, glabrous, green, rugose.

Central America (Panama) and South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil, and Paraguay). In Venezuela, found in the Andes (Lara, Táchira, and Trujillo) and in the Cordillera de la Costa (Carabobo and Yaracuy; Map 21). Park records are from cloud forest on the north slope of Guaramacal; 1,850 m.

COMMON NAME. Laurel blanco.

Branches and leaves are fragrant when crushed.

There is a report (van der Werff, 2008) that *Endlicheria paniculata* occurs in Amazonas state but without having examined a voucher we refrain from including this record in our distributional summary or map.

**MAP 21.** Distribution of *Endlicheria paniculata*.

## *Nectandra* Rol. ex Rottb.

*Nectandra* Rol. ex Rottb., Acta Lit. Univ. Hafn. 1: 279. 1778, nom. cons.

Trees or shrubs. Leaves alternate, rarely partly opposite, penninerved, rigid or chartaceous; axillary hairs or pit domatia rarely present. Inflorescences thyrso-paniculate, in axils of foliage leaves (rarely in axils of cataphylls), usually many-flowered. Flowers bisexual; tepals 6, in 2 rows, equal or subequal (outer ones larger), united at the base, ± spreading at anthesis, papillose internally; fertile stamens 9, ± papillose, in 3 whorls with 4-locular anthers, arranged in an arc or rarely in 2 pairs, 3 interior stamens with 2 glands at the base of the filaments; anthers introrse in whorls I and II, extrorse (or subextrorse) in whorl III; staminodes 3, in a separate whorl (whorl IV), often with a glandular patch, free or ± united with the filaments of the inner stamens; ovary globose. Fruit a 1-seeded berry, globose or ellipsoid; cupule almost always bowl-shaped, margin simple; tepals deciduous.

A Neotropical genus of ~100–115 species of which ~20 occur in Venezuela. The genus is found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay). Centers of diversity include the eastern slopes of the Andes and southeastern Brazil.

REFERENCES. Rohwer (1993b); Trofimov et al. (2016).

*Nectandra* and *Ocotea* are very similar and easily confused in the field. The morphological characters most useful for separating the two genera concern the tepals. Those of *Nectandra* species are papillose internally while those of *Ocotea* are pubescent or glabrous but not papillose. Also, in *Nectandra* the tepals are united at the base and detach as a unit while those of *Ocotea* are free and fall individually. Consequently, the young fruit of *Nectandra* lack tepals attached to the cupule while, with some exceptions, tepals persist on the young fruit of *Ocotea*.

### KEY TO THE SPECIES OF *NECTANDRA*

1a. Young branches and leaves below densely ferruginous-tomentose . . . . . ***N. laurel***
1b. Young branches and leaves below glabrous or sparingly to moderately ferruginous-tomentose or pubescent. . . . . 2
2a. Petioles 0.3–1 cm long; leaf blades 5–12 × 3–6.5 cm, secondary veins 6–12 each side of the midrib. . . . . **N. sp. A**
2b. Petioles 1–2.5 cm long; leaf blades 15–23 × 5–10.5 cm; secondary veins 5–8 each side of the midrib. . . . . ***N.* sp. B**

***Nectandra laurel*** Klotzsch ex Nees, Linnaea 21: 505. 1848.

*Persea peruviana* auct., non Nees; Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 320. 2010.

Trees, 8–10(–25) m tall; branchlets angular in cross-section, densely ferruginous-tomentose; terminal buds ovate to elongate, densely ferruginous-tomentose. Leaves elliptic to ovate, 5–15 × 3–6 cm, base usually obtuse, margin very slightly revolute, apex obscurely or sharply acuminate, ferruginous-pubescent throughout, quickly becoming glabrous above except for venation, secondary veins 6–9 each side of the midrib, impressed above, prominent below, coriaceous; petioles 1.8–2.5 cm long, often flattened in young leaves. Inflorescences 5–12 cm long, densely ferruginous-tomentose; peduncles 5–7 cm long. Flowers fragrant; tepals ± elliptic, white, papillose on inside surface; stamens of whorls I and II ~1.7 mm long; anthers broadly ovate, obtuse, the connective tissue papillose; staminodes ~0.3 mm long; ovary ovoid or obovoid, ~2.3 mm tall, glabrous; stigma

obtuse, discoid. Fruit ellipsoid, 10–12 × 6–8 mm, smooth, green; cupule green with red spots.

Known only from South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, found in the Andes (Barinas, Lara, Mérida, Portuguesa, Táchira, and Trujillo) and in the Cordillera de la Costa (Aragua, Distrito Capital, Monagas, and Sucre; Map 22). In the park, found in cloud forest on both slopes of Guaramacal; 1,500–2,100 m.

A sterile collection (*Cuello et al. 976*), which was reported by Dorr et al. (2000) as "cf. *Persea peruviana* Nees," appears to represent the juvenile foliage of *Nectandra laurel*. The collection does not agree with any of the *Persea* taxa known from Guaramacal nor recognized by Ferrer-Pereira (2012).

### *Nectandra* sp. A

Trees, 8–25 m tall; terminal branchlets striate, glabrous or sparingly tomentose-ferruginous; terminal or axillary buds pyramidal, 9–12 mm long, minutely tomentose or appressed pubescent. Leaves almost always elliptic, sometimes ovoid, 5–12 × 3–6.5 cm, base cuneate, rounded, or obtuse, apex acuminate with a 1–1.5 cm long tip, sometimes rounded, glabrous above and below, secondary veins 6–12 each side of the midrib, prominent below, impressed or sunken above, sometimes the principal veins below minutely tomentose; petioles flat, sometimes winged, 0.3–1 cm long, minutely tomentose or smooth, dark brown or almost black when dry. Flowers and fruit unknown.

At present, known only from Guaramacal National Park in Venezuela (Trujillo; Map 23). Found in cloud forest on the north slope of Guaramacal; 2,300–2,600 m.

We have not collected flowers or fruit of this taxon (one collection consists of empty cupules gathered from the ground). Our description is based on four sterile collections, the last of which was collected in 2000. Recent attempts to collect fertile material have been unsuccessful leading us to assume that flowering is erratic, at best.

**MAP 22.** Distribution of *Nectandra laurel*.

**MAP 23.** Distribution of *Nectandra* sp. A.

### *Nectandra* sp. B

*Nectandra membranacea* auct., non (Sw.) Griseb.; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 317. 2010.

Trees, 12–15 m tall; twigs ± angular or ridged in cross-section, moderately to sparsely pubescent, hairs predominantly appressed; terminal buds ovoid, densely appressed pubescent. Leaves elliptic to lanceolate or ovate-elliptic, 15–23 × 5–10.5 cm, base attenuate, apex acuminate, secondary veins 5–8 each side of the midrib, midrib, secondary, and tertiary veins immersed above, midrib and secondary veins raised below, sparsely appressed pubescent to glabrous above and below, chartaceous; petioles 1–2.5 cm long. Flowers and fruit unknown.

At present, known only from Guaramacal National Park in Venezuela (Portuguesa and Trujillo; Map 24). Found in cloud forest on both slopes of Guaramacal; 1,500–2,200 m.

Our vouchers for this taxon are all sterile and probably represent juvenile rather than mature foliage. We have not yet matched these collections to any species of *Nectandra* known from the Venezuelan Andes.

## *Ocotea* Aubl.

*Ocotea* Aubl., Hist. Pl. Guiane 2: 780. 1775.

Trees or shrubs. Leaves alternate, rarely crowded at the tips of branches, usually penninerved, rarely subtriplinerved; domatia sometimes present. Inflorescences thyrso-paniculate, rarely racemose, borne in the axils of leaves or (rarely) deciduous cataphylls. Flowers bisexual or unisexual (plants hermaphroditic,

**MAP 24.** Distribution of *Nectandra* sp. B.

polygamous, or dioecious), small; tepals 6, ovate, equal, erect, spreading or reflexed at anthesis; fertile stamens 9, whorls I–III fertile, whorl IV staminodial or lacking; filaments usually present. Staminate flowers: anthers 4-locular (rarely 2-locular), outer 6 introrse, inner 3 extrorse; inner 3 stamens with glands at the base of filaments; staminodes present or absent, if present 3, stipiform and small, with or without a pistillode. Pistillate flowers: 9 staminodes present; ovary (partly) enclosed in the floral tube. Fruit a 1-seeded berry; cupule present, variable, mostly cup-shaped with a single margin, but occasionally with a double margin or reduced to a small plate; tepals rarely persisting on the rim of cupules.

A genus of ~350(–515) species found in the Neotropics, Africa, and Madagascar. Most species (~300) occur in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay). Approximately 100 species are found in Venezuela.

REFERENCES. Rohwer (1986); van der Werff (2002a, 2013, 2014, 2020); Trofimov et al. (2019, 2022); Trofimov and Rohwer (2020); Penagos Zuluaga et al. (2021).

Molecular data (Chanderbali et al., 2001; Chanderbali, 2004; Rohwer et al., 2009; Trofimov et al., 2016, 2019; Rohde et al., 2017; Penagos Zuluaga et al., 2021) indicate that *Ocotea* as traditionally circumscribed is paraphyletic with respect to numerous other widely accepted genera. The taxonomic solution is to either recognize one large genus or to dismember *Ocotea* s.l. so that many previously proposed genera can be maintained. The trend seems to favor the latter solution. Nonetheless, we seem to be far from having a widely accepted and stable taxonomy for Neotropical *Ocotea* and relatives.

Species of *Ocotea* can be confused with species of *Andea*, *Damburneya*, and *Nectandra* (q.v.). They also can be confused with species of *Cinnamomum*, but this last genus has relatively larger staminodes with glandular apices and trinerved leaves, and furthermore it has not beeen reported from the park. Species of *Ocotea* with unisexual flowers can be confused with *Endlicheria*, which has 2- or 4-locular anthers.

## KEY TO THE SPECIES OF *OCOTEA*

1a. Leaves with 12–16 secondary veins each side of the midrib . . . . . **O. sp. D**
1b. Leaves with 4–12 secondary veins each side of the midrib . . . . . 2
2a. Petioles terete or flat, never sheathing or channeled . . . . . 3
3a. Lower surface of leaves covered by a dense, appressed indumentum . . . . . 4
4a. Leaf blades broadly elliptic to slightly obovate, 3.5–7.3 × 2–4 cm; 7–9 secondary veins each side of midrib . . . . . ***O. guaramacalensis***
4b. Leaf blades broadly elliptic, 10–18(–23) × 6–12 cm; 8–12 secondary veins each side of midrib ***O. terciopelo***
3b. Leaves glabrous or lacking a dense tomentose indumentum below . . . . . 5
5a. Leaves 10–16(–25) × 5–8 cm, minute black (glandular?) dots above and below . . . . . ***O. puberula***
5b. Leaves 2.5–16 × 3–6 cm, without minute black dots . . . . . 6
6a. Terminal branches sparsely pubescent to glabrous, without appressed hairs; midrib glabrous below, secondary veins flush or impressed below . . . . . ***O. floribunda***
6b. Terminal branches pubescent with appressed hairs; midrib sometimes slightly pubescent below, secondary veins prominent below . . . . . **O. sp. E**
2b. Petioles sheathing or channeled (canaliculate) . . . . . 7
7a. Terminal branches angular in cross-section or sometimes winged . . . . . 8
8a. Terminal branches winged, glabrous or with a few whitish hairs; buds or new shoots elongated, 2–3.5 cm long, bright white tomentose . . . . . **O. sp. B**
8b. Terminal branches angular in cross-section, ferruginous-tomentose; buds or new shoots short, 0.2–0.3 cm long, ferruginous tomentose . . . . . ***O. leucoxylon***
7b. Terminal branches terete or angular in cross-section, never winged . . . . . 9
9a. Leaf blades ovate or broadly lanceolate, base obtuse; petioles 1–2 cm long . . . . . ***O. vaginans***

9b. Leaf blades elliptic or elliptic-lanceolate, base acute, attenuate, or acuminate; petioles 0.5–1.5 cm long . . . .10
10a. Leaves with minute black (glandular?) dots above . . . . . ***O. leptobotra***
10b. Leaves without minute black dots . . . . . .11
11a. Leaves with 5–8 secondary veins on each side of the midrib; midrib, secondary, and tertiary veins raised below . . . . . **O. sp. C**
11b. Leaves with 7–10 secondary veins on each side of the midrib; midrib raised and secondary veins flush or slightly raised below . . . . . **O. sp. A**

*Ocotea floribunda* (Sw.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 325. 1889; van der Werff, in Berry et al., Fl. Venez. Guayana 5: 735. 1999. *Laurus floribunda* Sw., Prodr. 65. 1788.

Dioecious trees, (3–)7.5–20(–30) m tall; branchlets terete or angular in cross-section, solid, very sparsely pubescent to glabrous; terminal buds elongate pyramidal, densely appressed pubescent. Leaves alternate, elliptic-lanceolate, or obovate, 4–9 × 3–4 cm, base cuneate, slightly decurrent on petiole, margin entire, slightly revolute near base, apex acute or acuminate, glabrous, secondary veins 6–9 each side of the midrib, finely reticulate-veined above and below, secondary veins flush or slightly impressed above, chartaceous to coriaceous; domatia absent; petioles 3–12 mm long, channeled (canaliculate). Inflorescences paniculate-cymose, axillary, 5–15 cm long, sparsely to densely pubescent. Flower buds yellow (fide *Cuello 1152*). Flowers unisexual, greenish white. Staminate flowers: ~5 mm in diameter, stamens 9, all 4-locular; filaments of outer 6 with a few hairs or glabrous, filaments of inner 3 with some appressed hairs or glabrous; 2 glands at base of inner stamens; pistillode slender; stigma well-developed. Pistillate flowers: tepals spreading, outer surface sparsely to densely pubescent, inner surface glabrous to densely pubescent; staminodes 9, glands at base of inner staminodes; pistil glabrous; stigma conspicuous, discoid; receptacle glabrous within. Fruit globose or ellipsoidal, 1–1.6 cm in diameter, ± glaucous; peduncles 0.9–3 cm long; cupule green or reddish, flat or plate-like and with an irregular double margin; tepals sometimes persisting.

This species occurs in Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, and Paraguay). Widespread in Venezuela (Amazonas, Aragua, Barinas, Bolívar, Delta Amacuro, Distrito Capital, Mérida, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, and Zulia; Map 25). Our collections are from cloud forest on both slopes of Guaramacal; 1,600–2,400 m.

The wood is fragrant.

The fruits and cupules of this species are distinctive. The large globose or ellipsoidal fruits are seated on a flat or plate-like cupule with an irregular double margin.

**MAP 25.** Distribution of *Ocotea floribunda*.

♦ ***Ocotea guaramacalensis*** van der Werff, Novon 22: 347, fig. 5. 2013.

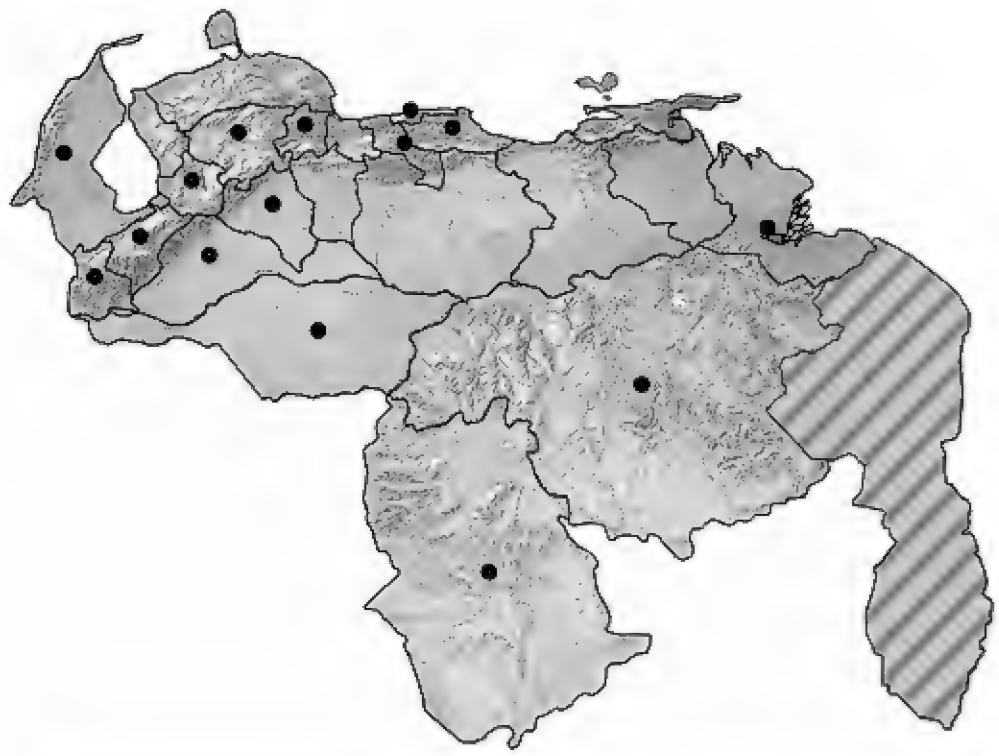
*Ocotea jelskii* auct., non Mez; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 318. 2010.

Trees, to 35 m tall; twigs terete, solid, densely and minutely appressed pubescent; terminal buds densely appressed pubescent, hairs often pale brown. Leaves alternate, broadly elliptic to slightly obovate, 3.5–7.5 × 2–4 cm, base acute or obtuse, margin entire, not revolute, apex obtuse or with a short apical tip 4–6 mm long, glabrous above, covered by a dense, appressed, pale brown indumentum below, secondary veins 7–9 on each side of the midrib, venation immersed on the upper surface, the secondary veins scarcely visible, midrib and secondary veins slightly raised on the lower surface, tertiary venation immersed, coriaceous; domatia absent; petioles 4–6 mm long, flat above, minutely appressed pubescent. Inflorescences paniculate-cymose, axillary, 5–8 cm long, densely tomentellous. Flower buds ferruginous. Flowers bisexual, ~5 mm in diameter, greenish-yellow; pedicels to 1.5 mm long, densely tomentellous; tepals 6, 1.5–3.1 mm long, spreading, pubescent on the outer and inner surfaces, papillose toward the margin; stamens 9, all 4-locular, outer 6 stamens ~1 mm tall, glabrous or with a few hairs on the very short filaments, inner 3 stamens ~1 mm tall, glands at base of inner stamens; staminodes ~0.5 mm tall, stipitiform, with a few hairs; pistil 1.7 mm tall, glabrous; receptacle deep, densely pubescent inside. Infructescences to 12 cm long; old cupules cup-shaped, with a single margin, 1.2 ×1.5 cm. Fruit unknown.

Endemic to Venezuela, where it is found only in the Andes (Trujillo; Map 26). In the park, found in cloud forest on the north slope of Guaramacal; 2,400–2,700 m.

The foliage is fragrant when crushed.

MAP 26. Distribution of *Ocotea guaramacalensis*.



MAP 27. Distribution of *Ocotea leptobotra*.

***Ocotea leptobotra*** (Ruiz & Pav.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 376. 1889. *Laurus leptobotra* Ruiz & Pav., Laurographia t. 368. [1804–]1813.

*Oreodaphne cernua* Nees, Syst. Laur. 424. 1836. *Ocotea cernua* (Nees) Mez, Mitt. Bot. Vereins Kreis Freiburg 47–48: 422. 1888; van der Werff, in Berry et al., Fl. Venez. Guayana 5: 733. 1999; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001]; Wingfield and van der Werff, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 532. 2007.

Dioecious trees, 5–8 m tall; young branchlets somewhat angular in cross-section or terete, solid, glabrous; terminal buds densely appressed pubescent. Leaves alternate, elliptic to elliptic-lanceolate, 8–14 × 3.5–5 cm, base acute, apex acuminate or caudate, apical tip 1.5–2 cm long, often curved or falcate, glabrous with minute black (glandular?) dots above (visible when dry), 6–8 secondary veins on each side of the midrib, veins slightly prominent below, chartaceous; domatia absent; petioles 0.6–1.5 cm long. Inflorescences paniculate-cymose, axillary, 5–10 cm long, glabrous, segments pendulous or slightly reflexed. Flowers unisexual, reddish in bud, yellowish green at anthesis, lemon-scented; tepals 6, ~2 mm long, glabrous on both surfaces, ± erect at anthesis. Staminate flowers: stamens 9, glabrous, 4-locular, outer 6 with filaments ± fused to tepals, inner 3 with glands at base; pistillode minute or lacking. Pistillate flowers: staminodes 9, inner 3 with glands at base; pistil ~1.5 mm long, glabrous; style short; ovary well-developed. Cupule distinctly cup-shaped, ~10 mm in diameter, smooth, red when mature; fruit ovoid, 1.4 × 0.9 cm, black when mature.

Found in Mexico, Central America, the West Indies (Windward Islands), and South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, and Brazil). Widespread in Venezuela (Amazonas, Apure, Aragua, Barinas, Bolívar, Delta Amacuro, Distrito Capital, Lara, Mérida, Miranda, Portuguesa, Táchira, Trujillo, Yaracuy, and Zulia; Map 27). This tree has been collected near the lower limits of the park on the south slope of Guaramacal in remnants of cloud forest; 1,500–1,550 m.

*Laurus leptobotra* was validly published as a plate with analysis in July 1813 or possibly earlier (see discussion regarding date following *Damburneya purpurea*).

***Ocotea leucoxylon*** (Sw.) Laness., Pl. Util. Col. Franç. 158. 1886; van der Werff, in Berry et al., Fl. Venez. Guayana 5: 736, fig. 620. 1999. *Laurus leucoxylon* Sw., Prodr. 65. 1788 ("*Leucoxylon*").

*Ocotea lasseriana* C. K. Allen, Mem. New York Bot. Gard. 10(5): 90. 1964.

Trees, 4–24 m tall; crown rounded, not spreading; young stems angular in cross-section, solid, densely appressed pubescent, ferruginous when dry. Leaves alternate, elliptic to oblong, 7–17(–22) × 2.5–7 cm, base acute to obtuse, margin sometimes slightly revolute, apex acute to acuminate with a 5–10 mm long tip, glabrous above, minutely appressed pubescent below, pinnately veined, secondary veins 6–10 on each side of the midrib, midrib, secondary and tertiary veins immersed above, midrib and secondary veins raised below, chartaceous; domatia absent; petioles 1–2.5 cm long, canaliculate. Inflorescences axillary, paniculate-cymose, 4–12 cm long, densely appressed pubescent. Flowers unisexual; buds green; flowers (at anthesis) white, 3–4 mm in diameter. Staminate flowers: tepals 6, glabrous on outer and inner surface, spreading; stamens 9, all 4-locular, outer 6 glabrous, inner 3 with glands at base; pistillode slender, glabrous; stigma discoid, small; receptacle deeply cup-shaped, pubescent. Pistillate flowers: tepals glabrous or sparsely pubescent on outer surface, glabrous on inner surface; staminodes 9, inner 3 with 2 glands at base; pistil glabrous; stigma discoid; receptacle deeply cup-shaped, glabrous inside. Cupules bowl-shaped, warty or lenticellate, 6–8 mm in diameter; fruit globose or

subglobose, 6–12 mm in diameter with a tiny apical tip 0.5–1.5 mm tall; tepals deciduous in fruit.

Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, and Brazil). In Venezuela, found in the Andes (Lara, Portuguesa, Táchira, and Trujillo), the Cordillera de la Costa (Aragua, Carabobo, Distrito Capital, Falcón, Nueva Esparta, and Yaracuy), and the Venezuelan Guayana (Amazonas, Bolívar, and Delta Amacuro; Map 28). Cloud forest on both slopes of Guaramacal; 1,500–2,400 m.

This species can be recognized by its gray-green leaves that are smooth above and minutely appressed pubescent below, distant (versus clustered) inflorescences, small unisexual flowers, and warty or lenticellate cupules.

***Ocotea puberula*** (Rich.) Nees, Syst. Laur. 472. 1836; van der Werff, in Berry et al., Fl. Venez. Guayana 5: 737. 1999. *Laurus puberula* Rich., Actes Soc. Hist. Nat. Paris 1: 108. 1792 ("*Puberula*").

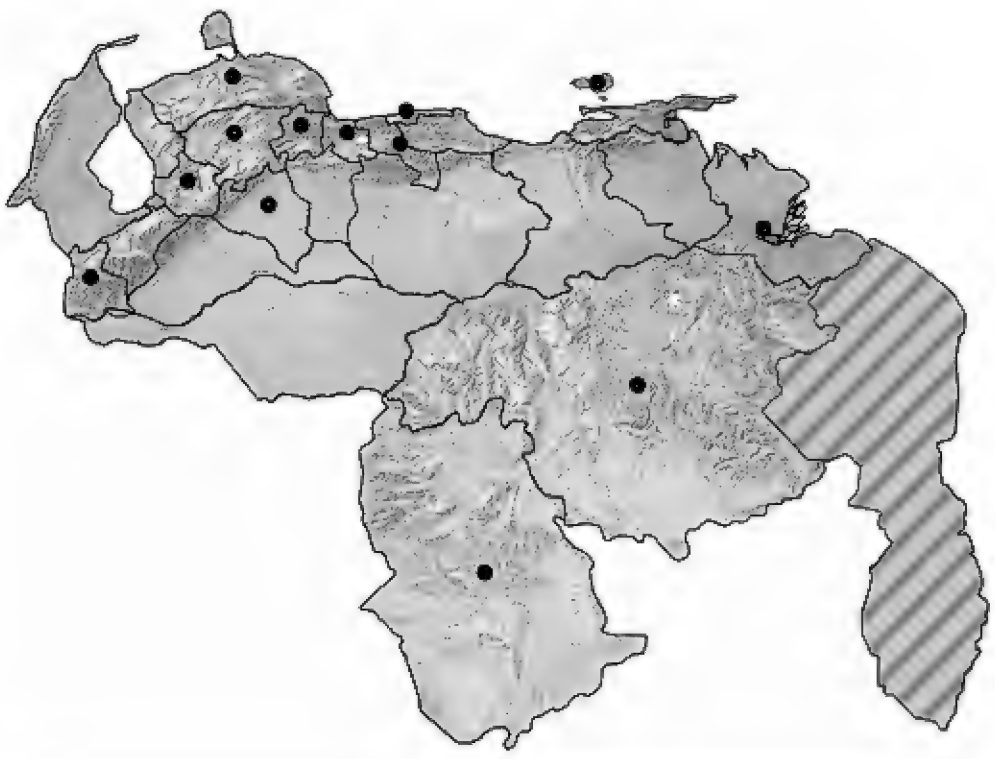
Trees, 5–15 m tall; branchlets terete or somewhat angular in cross-section, solid, glabrous or sparsely to moderately appressed pubescent; terminal buds densely appressed pubescent. Leaves alternate, elliptic or broadly elliptic, 10–16(–25) × 5–8 cm, base acute to obtuse, margin sometimes revolute at base only, apex obtuse to acuminate, minute black (glandular?) dots above and below, glabrous above and below or with a few appressed hairs below, slightly glaucous below, pinnately veined, secondary veins 6–10 each side of the midrib, midrib and secondary veins slightly prominent above and below, (thinly) chartaceous; domatia absent; petioles 1–2 cm long, sometimes winged, almost always glabrous. Inflorescences axillary, paniculate-cymose, 4–15 cm long. Flowers unisexual, 4–5 mm in diameter, pale green; tepals 2–2.5 mm long, widely ovate, glabrous or with some appressed hairs near the exterior base. Staminate flowers: tepals 6, glabrous or with appressed hairs near base outside, subglabrous to moderately pubescent inside; stamens 9 (6 outer, 3 inner), 4-locular, glabrous; 2 globose glands at base of filaments; pistillode glabrous; receptacle shallow, glabrous inside. Pistillate flowers: tepals 6, glabrous or with appressed hairs near base outside, subglabrous to moderately pubescent inside; staminodes 9, glabrous; glands at base of inner 3 staminodes; pistil glabrous; stigma capitate; receptacle bowl-shaped, glabrous inside. Cupules plate-like, 6–8 mm in diameter, not lenticellate, margin single; fruit subglobose, ~8 mm in diameter; tepals deciduous in fruit.

Mexico, Central America, and South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay). In Venezuela, found in Amazonas, Apure, Bolívar, Distrito Capital, Mérida, Portuguesa, Táchira, Trujillo, and Zulia; Map 29). In the park, known from cloud forest on both slopes of Guaramacal; 1,500–2,100 m.

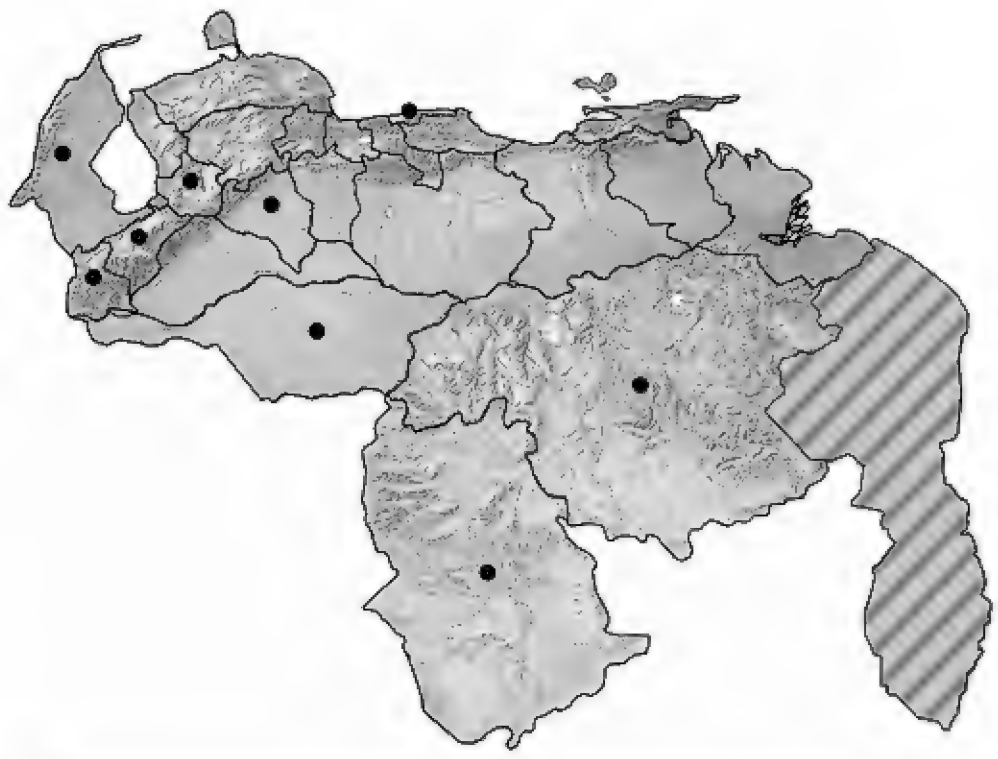
Van der Werff in Berry et al. (1999) restricted the distribution of this species in Venezuela to Amazonas and Bolívar states. Subsequently, van der Werff (2020) included *Ocotea puberula* among the Andean species with unisexual flowers and cited material from Mérida but provided no explanation for the change in how he interpreted its geographical range.

***Ocotea terciopelo*** C. K. Allen, Mem. New York Bot. Gard. 15: 75, fig. 8. 1966.

Trees, 9–20 m tall; trunk straight; crown small (fide *van der Werff et al. 7622*); branchlets distinctly angular in cross-section, solid, densely ferruginous-tomentose, glabrate in age; terminal buds densely ferruginous-tomentose. Leaves alternate, broadly elliptic, 10–18(–23) × 6–12 cm, base obtuse or acute, margin plane to slightly incurved, apex acute or rounded, glabrous above, densely ferruginous-tomentose below, 8–12 secondary



**MAP 28.** Distribution of *Ocotea leucoxylon*.



**MAP 29.** Distribution of *Ocotea puberula*.

veins each side of the midrib, midrib raised above to the middle of the leaf, then ± impressed, secondary veins impressed, midrib and secondary veins prominent below, rugose, coriaceous; petioles 5–12 mm long, winged, ferruginous-tomentose. Inflorescences axillary, 15–20 cm long, densely ferruginous-tomentose. Flowers bisexual, ~7 mm in diameter; pedicels ~2–4 mm long, pubescent; tepals 6, spreading, densely pubescent on both surfaces; stamens 9 (6 outer, 3 inner), all 4-locular, glabrous; glands at base of inner stamens; staminodes present, stipitiform, glabrous; pistil ~2 mm tall, glabrous. Cupules disc-shaped, margin single with obscure teeth; fruit ovoid, ~2 × 1.5 cm.

Restricted to northern Andean South America (Colombia and Venezuela). In Venezuela, found in the Andes (Lara, Portuguesa, Táchira, and Trujillo; Map 30). In the park, known from cloud forest on both slopes of Guaramacal, including near La Divisoria de la Concepción; 1,700–2,350 m.

COMMON NAME. Laurel cantarito.

USE. The wood is used in the construction of houses (fide *van der Werff et al. 7622* in sched.).

This distinctive species, described from Lara, is easy to recognize in the field by its relatively large (~18–23 cm long) rugose leaves that are coriaceous with ferruginous pubescence below and by its relatively short (5–12 mm long) winged petioles.

***Ocotea vaginans*** (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 245. 1889. *Mespilodaphne vaginans* Meisn., in de Candolle, Prodr. 15(1): 104. 1864.

Trees, 6–16 m tall; young stems tomentose pubescent, angular in cross-section, sometimes hollow; terminal buds tomentulose. Leaves alternate or subopposite, ovate or broadly lanceolate, 10–15 × 5–10 cm, base obtuse, margin plane, apex sharply acuminate or acute, glabrous above and below, secondary veins 8–12 each side of the midrib, midrib and secondary veins sightly impressed above, some secondary veins also slightly prominent, veins raised below, coriaceous; domatia absent; petioles canaliculate to vaginate, 1–2 cm long, minutely appressed pubescent. Inflorescences densely paniculate, tomentose, grayish, shorter than the leaves; pedicels to 4 mm long. Flowers bisexual, ~4 mm in diameter; tepals ovate, acute; filaments and anthers densely tomentose; internal whorl of anthers (series III) with large, sessile globose glands; staminodes absent or well-developed; ovary glabrous, ellipsoid; stigma obtuse. Fruit unknown.

Endemic to Venezuela, where it is known from the Andes (Trujillo) and the Cordillera de la Costa (Aragua and Distrito Capital; Map 31). In the park, collected in cloud forest on the south slope of Guaramacal; 1,950 m.

The presence of this species in the park and in Trujillo state is based on a single sterile collection (*Cuello et al. 1290*). The leaves, especially their bases, are distinctive. Several other sterile collections (*Cuello et al. 2037*, *2060*, *2111*) previously identified in Dorr et al. (2000) as *Ocotea vaginans* are probably not Lauraceae. *Ocotea vaginans* was omitted from the list of Andean species of *Ocotea* compiled by van der Werff (2020). Our description, in part, is taken from Bernardi (1962).

### *Ocotea* sp. A

*Ocotea neesiana* auct., non (Miq.) Kosterm.; Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001].

*Ocotea* sp. A (p.p.); Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001] (as to *Cuello et al. 1295*, *1867*).

Trees, to 5 m tall. Young branchlets and buds appressed pubescent. Leaves elliptic to oblong, 6–12.5 × 2–4 cm, base cuneate, apex generally acuminate, apical tip to 2.5 cm long, glabrous above, glabrescent or with appressed hairs below especially on veins, secondary veins 7–10 each side of the midrib, ascending at a 45–60° angle, veins impressed above,

**MAP 30.** Distribution of *Ocotea terciopolo*.

**MAP 31.** Distribution of *Ocotea vaginans*.

midrib raised and secondary veins flush or slightly raised below; petioles 4–11 mm long, flattened, involute when dry, appressed pubescent or glabrous. Floral branches and flower buds appressed pubescent.

At present, known only from Guaramacal National Park in Venezuela (Portuguesa and Trujillo; Map 32). In the park, found on the south slope of Guaramacal, including near La Divisoria de la Concepción; 1,500–1,950 m.

The taxon described here has only been collected in very young bud.

### *Ocotea* sp. B

*Ocotea auriculata* auct., non Lasser; Dorr et al., Contr. U.S. Natl. Herb. 40: 103. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 318. 2010.

Trees, to 15 m tall; apical branchlets quadrangular in cross-section, winged, glabrous or with a few whitish hairs; prophylls persistent, tomentose or diminutively appressed pubescent. Leaves oblanceolate or obovoid, 12–22.5 × 5–9 cm, base attenuate or acute, apex rounded or acute, glabrous above, glabrescent below or with a few appressed hairs especially at base and on veins, secondary veins 8–12 each side of the midrib, midrib and secondary veins impressed above, raised below; domatia in axils of midrib and secondary veins below; petioles 1.5–2.5 cm long, flattened-winged, convolute, glabrous or sometimes slightly appressed pubescent. Flower buds whitish (fide *Cuello et al. 1178*).

At present, known only from a single collection in very young bud made in Guaramacal National Park in Venezuela (Trujillo; Map 33). Found on the north slope of Guaramacal; 1,850 m.

This taxon is similar to *Ocotea auriculata* Lasser but differs in not having the base of its leaves auricled, which defines the latter species.

**MAP 33.** Distribution of *Ocotea* sp. B.

### *Ocotea* sp. C

*Ocotea* aff. *tarapotana* auct., non (Meisn.) Mez; Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 319. 2010.

Small trees, to 3 m tall; terminal branchlets appressed-tomentose; buds densely pubescent. Leaves elliptic to lanceolate, 8–14 × 2–4 cm, base cuneate, apex acuminate with a 1–2.5 cm long tip, glabrous or the midrib appressed pubescent in its lower half, secondary veins, 5–8 each side of the midrib, midrib and secondary veins impressed above, veins raised below; petioles short, 5–10 mm long, involute or caniculate, pubescent.

**MAP 32.** Distribution of *Ocotea* sp. A.

**MAP 34.** Distribution of *Ocotea* sp. C.

At present, known only from a single collection (*Cuello et al. 1799*) made in Guaramacal National Park in Venezuela (Portuguesa; Map 34). In the park, found in forest on the south slope of Guaramacal; 1,650–1,700 m.

Our material of this taxon is sterile and after further study our earlier determination (Dorr et al., 2000) does not seem justified especially as the leaves of *Ocotea tarapotana* are glabrous and only have 2–3(–4) secondary veins each side of the midrib that anastomose unlike this unnamed taxon.

### *Ocotea* sp. D

*Ocotea terciopelo* auct., non C. K. Allen; Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001] (as to *Cuello et al. 2086*).

Trees, 9 m tall; branchlets striate, solid, glabrous or sparingly tomentose; terminal buds pyramidal, ferruginous-tomentose. Leaves ovate to orbicular, 15–25 × 10–15 cm, base attenuate or acute, apex acuminate with a 5–15 mm long tip, glabrous above and below or with appressed hairs the length of the veins below, 12–16 secondary veins each side of the midrib, erect-ascending, diverging at 30–45° from the midrib, midrib striate at the base and slightly raised from base to mid-part of the leaf blade, secondary veins slightly raised, coriaceous; petioles 5–10 mm long, flattened, winged, 3–4 mm thick, glabrous or pubescent.

At present, known only from a collection made in Guaramacal National Park in Venezuela (Trujillo; Map 35). Found in cloud forest on the north slope of Guaramacal; 2,350 m.

Our sterile voucher (*Cuello et al. 2086*) for this taxon does not agree completely with *Ocotea terciopelo* and may represent a distinct species.

### *Ocotea* sp. E

Trees, 18–25 m tall; branchlets solid with appressed hairs; terminal buds densely pubescent. Leaves elliptic, 7–16 × 4–6 cm, base obtuse or acute, apex acuminate or acute, glabrous above but with readily visible gland dots, sometimes midrib slightly pubescent, secondary veins 5–9 each side of the midrib, midrib and secondary veins slightly raised above, especially the base of the midrib, veins prominent below, chartaceous; domatia present in axils of midrib and secondary veins below; petioles 4–10 mm long, flat, sometimes involute or winged, almost always tomentose pubescent, axillary buds 2–3 mm tall. Inflorescences to 6 cm long, moderately pubescent; bracts ferruginous. Flowers ~3 mm in diameter. Fruit globose or ellipsoidal, 1.2 × 0.8 cm; shallow cupule widened apically, 1–2 cm long, 4–5 mm in diameter at the apex, margin smooth, crenate, rugose, woody, brown; tepals persistent.

At present, known only from collections made in Guaramacal National Park in Venezuela (Trujillo; Map 36). In the park, found in cloud forest on both slopes of Guaramacal; 1,600–2,100 m.

COMMON NAME. Laurel hediondo.

The wood is foul smelling (fide *Dorr et al. 8627* in sched.).

## *Persea* Mill.

*Persea* Mill., Gard. Dict. Abr., ed. 4 [1030]. 1754, nom. cons.
*Farnesia* Heist. ex Fabr., Enum., ed. 2, 400. 1763.
*Mutisiopersea* Kosterm., Rheedea 3: 133. 1993.

Trees and shrubs. Leaves alternate, generally distributed along the branches or sometimes clustered, pinnatinerved; domatia absent. Inflorescences axillary or in the axils of cataphylls, paniculate-cymose, lateral flowers of a cyme always opposite. Flowers bisexual; tepals 6, equal or not, when unequal the 3 external tepals smaller than the internal ones; tepals deciduous or persistent, when persistent the entire unit generally maintained; stamens 9 or 6, when 6, those of whorl III staminodial;

**MAP 35.** Distribution of *Ocotea* sp. D.

**MAP 36.** Distribution of *Ocotea* sp. E.

anthers almost always 4- rarely 2-locular; internal stamens with 2 globose glands at the base; staminodes of whorl IV with triangular or saggitate apices. Fruit pyriform or globose (oblate), generally with persistent tepals and stamens at the base; cupule never present.

A tropical and subtropical genus of ~100 species found in North America (USA), Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Chile, Paraguay, and Argentina), and the Canary Islands. Species of the genus are introduced in Africa and Asia. Major centers of diversity include Central America and northern South America. Twenty-four species are found in Venezuela.

REFERENCES. Kopp (1966); van der Werff (2002b); Rohwer et al. (2009); Li et al. (2011); Ferrer-Pereira (2012).

The genus *Persea* as presently construed is not monophyletic (Rohwer et al., 2009; Li et al., 2011). The type of the genus is *Persea americana* Mill., a species better known as the source of the edible and commercially important avocado or aguacate. This species originated in the highlands of Central America, but now is widely cultivated elsewhere in the Americas, including the Venezuelan Andes. Chanderbali et al. (2001) dismissed the implication that *Persea* might not by monophyletic, so it was somewhat surprising that Rohwer et al. (2009) resolved *P. americana* and closely related species as well-supported members of an otherwise Asian clade that includes species of *Alseodaphne* Nees and *Phoebe* Nees, and that this clade, in turn, was found to be distinct from a clade that contains most of the South American species currently assigned to *Persea* (Rohwer et al., 2009; Li et al., 2011). These South American species (*P.* subgen. *Eriodaphne* Nees) and the sole Macaronesian species, *P. indica* (L.) Spreng., form a moderately to strongly supported clade. As generic limits in the Lauraceae become better defined and more natural, this American-Macaronesian clade almost certainly will be recognized at generic rank and the Guaramacal species of *Persea* transferred to *Farnesia*.

## KEY TO THE SPECIES OF *PERSEA*

1a. Leaves below tomentose with pubescence covering 60–100% of the surface . . . . . 2
  2a. Shrubs, 1–3 m tall; leaf blades densely ferruginous-tomentose below; petioles 0.5–1.4 cm long . . . . . ***P. ferruginea***
  2b. Trees, 20–25 m tall; leaf blades tomentose below, but not ferruginous; petioles 1.5–6 cm long. . . . . ***P. caerulea***
1b. Leaves below glabrous or with hairs covering < 50% of the surface . . . . . 3
  3a. Branches glabrous; leaves with 10–14 secondary veins diverging from each side of the midrib at an angle ≤ 15–20° . . . . . **P. sp. A**
  3b. Branches glabrous or pubescent, or with dispersed hairs; leaves with 6–11 secondary veins diverging from each side of the midrib at an angle ≥ 30° . . . . . 4
    4a. Petioles > 4 mm wide at the base; inflorescences corymbiform, 5–7 cm long; flowers yellow. . . . . ***P. mutisii***
    4b. Petioles < 4 mm wide at the base; inflorescences in racemes or panicles, 10–25 cm long; flowers white or greenish white. . . . . 5
      5a. Branches glabrous or with dispersed whitish hairs; apical buds glabrous; leaves clustered at the apex of branches; flowers to 3 mm long, greenish white; fruit 2–3 cm in diameter. . . . . ***P. rigens***
      5b. Branches with yellowish or brownish hairs; apical buds appressed pubescent; leaves distributed along the length of branches; flowers 4–7 mm long, white; fruit 1.1–1.2 cm in diameter . . . . . ***P. meridensis***

***Persea caerulea*** (Ruiz & Pav.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 171. 1889; van der Werff, in Berry et al., Fl. Venez. Guayana 5: 744. 1999. *Laurus caerulea* Ruiz & Pav., Laurographia t. 350. [1804–]1813.

FIGURE 4F–H

*Persea laevigata* Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 2: 125. 1817; ibid. [qu.] 2: 157. 1817.

*Persea lignitepala* Lasser, Bol. Soc. Venez. Ci. Nat. 9(58): 177, fig. 1944.

Trees, 20–25 m tall; terminal branchlets angular in cross-section, solid, ferruginous pubescent. Leaves alternate, distributed uniformly along the length of branches, elliptic, ovate-elliptic, or ovate-oblong, 10–20 × 4–10 cm, base acute, obtuse or rounded, margin entire, apex acute or less commonly obtuse, glabrous above, tomentose pubescent below, secondary veins (12–)14–16 each side of the midrib, primary, secondary and tertiary veins immersed above, primary and secondary veins raised below, tertiary veins impressed, chartaceous; petioles 1.5–6 cm long, striate, glabrous or ferruginous-pubescent. Inflorescences 5–15 cm long, borne in axils of leaves on terminal branches, pubescent, pendulous, reddish. Flowers yellowish-green, 5–6 mm in diameter; pedicels 2–4 mm long; tepals unequal, external tepals ovate, 1–2 mm long, internal tepals oblong, 4.5–6 mm long, external tepals pubescent abaxially, glabrous adaxially, internal tepals densely pubescent. Stamens 9, 3.5–4 mm long; anthers 4-locular, ~1 mm tall, glabrous; filaments 2.5–3 mm long, pubescent; filaments of internal stamens with 2 glands attached 1 mm above the base; pistil glabrous, ~1 mm tall, tube pubescent internally. Fruit globose, 8–10 mm in diameter, dark blue, almost black, shiny.

Central America and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, this species is found in mountainous areas including the Andes (Barinas, Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Cordillera de la Costa

(Aragua, Carabobo, Distrito Capital, Falcón, Miranda, Monagas, and Zulia), and Nueva Esparta (Map 37). In the park, found on the north slope where it is common in the vicinity of the Laguna de Los Cedros; 1,800 m.

COMMON NAME. Laurel jovicó.

*Laurus caerulea* first was validly published as a plate with analysis in July 1813 or possibly earlier (see discussion regarding date following *Damburneya purpurea*).

The report by van der Werff (2008) that *Persea caerulea* occurs in the Venezuelan Guayana (Bolívar and Delta Amacuro states) may not be correct. The Bolívar record can be traced to Kopp (1966) who cited a collection (*Steyermark & Nilsson 757*, VEN) that Ferrer-Pereira (2012) subsequently included as a paratype of *P. lemensis* H. Ferrer & Sanoja. The source for the Delta Amacuro record, however, could not be traced.

*Persea caerulea* is characterized by its strongly unequal tepals (outer tepals shorter than inner ones) and small dark- or greenish-blue fruit.

Some farmers in the vicinity of the park have indicated to us that their livestock (cattle, sheep, and goats) die after eating the leaves of this species whose regeneration is very abundant at the beginning of the rainy season. For this reason, the tree has been eradicated from almost all localities adjacent to the national park.

***Persea ferruginea*** Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 2: 126. 1817; ibid. [qu.] 2: 159. 1817.

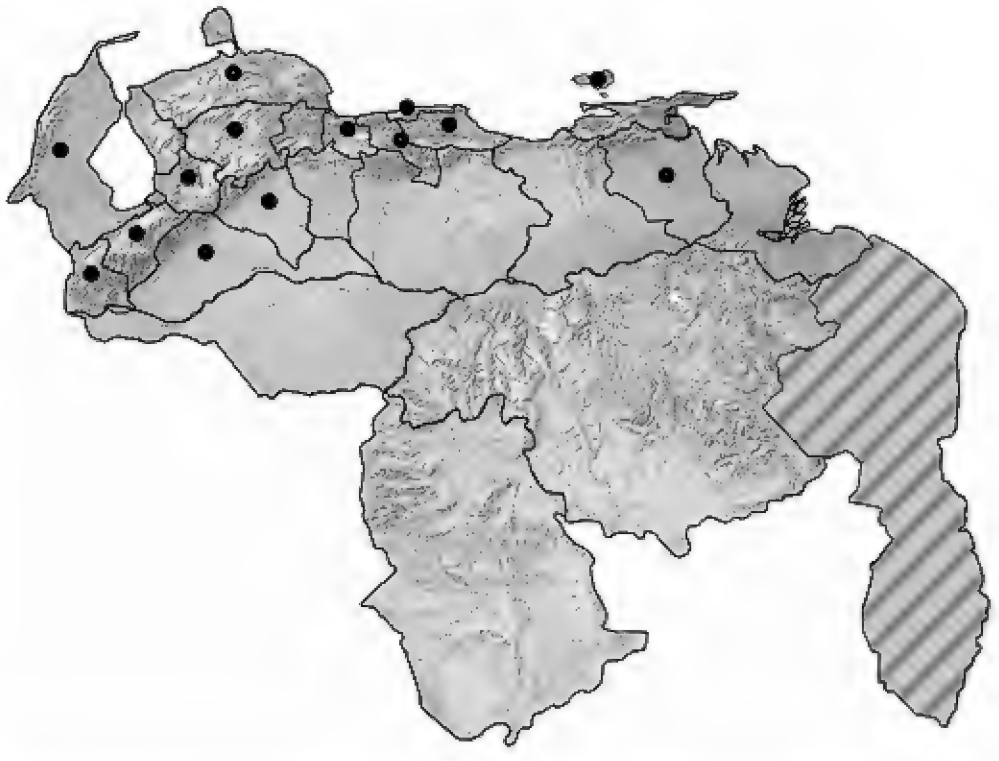
FIGURE 4I

Shrubs, 1–3 m tall; terminal branchlets angular in cross-section, solid, ferruginous-tomentose; apical buds short, ferruginous-tomentose. Leaves ovate to elliptic, 4–12 × 3.5–10 cm, base obtuse, slightly cordate or cuneate, margin entire, apex acute or obtuse, acuminate or rounded, 8–12 secondary veins each side of the midrib, the basal ones almost opposite, midrib slightly impressed above, other veins flush, glabrous above, midrib, secondary and tertiary veins raised below, densely ferruginous-tomentose below, coriaceous; petioles 0.5–1.4 cm long, plane or broadly caniculate. Inflorescences 4–12 cm long, tomentose; peduncles 3–4 mm long. Flowers yellow or greenish-pink, 5–6 mm long; tepals unequal. Fruit a berry, ellipsoid, ovoid or subglobose, 7–8 mm long; tepals and stamens persistent, pubescent.

Known only from South America (Colombia, Venezuela, Ecuador, Peru, and possibly Bolivia). In Venezuela, confined to the Andes (Lara, Mérida, Táchira, and Trujillo; Map 38). In the park, found in cloud forest, subpáramo, and páramo vegetation including along the Fila de Los Recortaderos and in the Páramo El Pumar (1,950–)2,350–3,100 m.

***Persea meridensis*** L. E. Kopp, Mem. New York Bot. Gard. 14(1): 81, fig. 7(4). 1966; Huérfano et al., Libro Rojo Fl. Venez., ed. 2, 281. 2020.

Trees, 6–15 m tall; branches angular in cross-section with yellowish or brownish hairs; buds with indumentum similar to that of branches. Leaves elliptic to oblanceolate, 10–19.5 × 3–7.8 cm, base acute or obtuse, margin slightly revolute either to the middle or for the total length of the blade, apex acute to acuminate, secondary veins 6–10 each side of the midrib, midrib sunken below, glabrous, veins almost always appressed pubescent below, often anastomosing, glaucous, hairs yellowish or brownish, coriaceous; petioles 2–3.5 cm long, channeled, < 4 mm wide at the base, glabrous or appressed pubescent. Inflorescences to 25 cm long, densely pubescent (reddish brown when dry). Flowers 4–7 mm long, white; tepals noticeably unequal, the inner ones larger, the outer ones with yellowish or brownish hairs especially dense on the abaxial face, internal tepals pubescent on both



**MAP 37.** Distribution of *Persea caerulea*.

**MAP 38.** Distribution of *Persea ferruginea*.

faces; fertile stamens in whorls I and II ovate, 1–1.2 × 0.5–0.8 mm; staminodes to 2 mm long, pubescent; ovary spherical or globose, 0.8–1 × 1–1.2 mm, glabrous. Fruit depressed-globose, 1.1–1.2 cm in diameter, green; pedicels 7 mm long, accrescent in fruit, gradually thickened toward the receptacle, rugose; tepals and stamens persistent, pubescent.

Endemic to Venezuela where it is found only in the Andes (Mérida, Portuguesa, and Trujillo; Map 39). In the park, it occurs in cloud forest on both slopes of Guaramacal, including La Divisoria de la Concepción; 1,700–2,750 m.

COMMON NAME. Aguacate jovicó.

The wood is fragrant.

According to Ferrer-Pereira (2012), collections of this species made in Portuguesa and Trujillo states, notably in and around Guaramacal National Park, have shorter and narrower elliptic to oblanceolate leaves with the pubescence varying in its extent, as well as axillary inflorescences much longer than the leaves. The substantial differences between these specimens and the holotype of *Persea meridensis*, indicate that the collections could be treated as a distinct species that is part of a variable complex surrounding *P. meridensis*.

***Persea mutisii*** Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 2: 126. 1817; ibid. [qu.] 2: 158. 1817 ("*Mutisii*"); Huérfano et al., Libro Rojo Fl. Venez., ed. 2, 282. 2020. *Mutisiopersea mutisii* (Kunth) Kosterm., Rheedea 3: 135. 1993.

*Persea pachytepala* Lasser, Bol. Soc. Venez. Ci. Nat. 9(58): 178. 1944.

Shrubs or trees, 4–10 m tall; branches angular in cross-section, glabrous or sometimes with hairs; apical buds short, glabrous or with indumentum similar to that of branches. Leaves generally elliptic, sometimes ovate or obovate, 5.2–22 × 3.5–11 cm, base obtuse, slightly cordate or cuneate, margin plane, apex obtuse, rounded, or acuminate, secondary veins 7–11 each side of the midrib, glabrous, rarely with hairs; petioles 0.7–2.5 cm long, flattened or caniculate, > 4 mm wide at the base, glabrous, rarely pubescent. Inflorescences corymbiform, 5–7 cm long. Flowers 3–7 × 3–4 mm, yellow; pedicels 1.5–2 mm long, thickened toward the receptacle; tepals noticeably unequal; stamens in whorls I and II ovate, 1.2–1.4 × 0.6–0.8 mm; filaments to 2 mm long, pubescent; anthers in whorl III triangular or trapezoidal, 1.0–1.4 × 0.4–0.6 mm; filaments to 2 mm long, pubescent, slightly larger or twice as large as the anthers, pubescent; staminodes sagittate, 0.8–1.2 mm long; ovary spherical or ellipsoid, 1–1.5 × 0.7–1.3 mm, glabrous; style 2–2.5 mm long. Fruit globose, 10–13 mm in diameter; peduncles 5–5.5 mm long; tepals and stamens persistent.

South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, known from the Andes (Apure, Barinas, Mérida, Táchira, and Trujillo) and the Cordillera de la Costa (Anzoátegui, Monagas, and Sucre; Map 40). In the park, found in cloud forest and subpáramo on the north slope of Guaramacal and along the Fila de Agua Fría; 2,550–2,800 m.

***Persea rigens*** C. K. Allen, J. Arnold Arbor. 26: 297. 1945; Huérfano et al., Libro Rojo Fl. Venez., ed. 2, 282. 2020.

The following weakly-defined variety is the only one found in Venezuela.

***Persea rigens*** var. ***oblaticarpa*** H. Ferrer, Hoehnea 39: 471, fig. 14. 2012.

Trees, 7(–30) m tall; branches terete, generally glabrous or with whitish hairs; terminal and axillary buds short, glabrous. Leaves clustered at the apex of branches, elliptic or ovate, 11–30 × 4–13.3 cm, base obtuse, rarely acute or cuneate, margin entire, apex acute, rarely obtuse or acuminate, glabrous or with whitish hairs above, sparsely pubescent below, midrib impressed above,

**MAP 39.** Distribution of *Persea meridensis*.

**MAP 40.** Distribution of *Persea mutisii*.

slightly wider in the lower half of leaf, glabrous, 8–10(–11) secondary veins each side of the midrib; petioles 1–2.8 cm long, flattened, glabrous. Inflorescences subterminal racemes, to 10 cm long. Flowers to 3 mm long, greenish white; pedicels 2.5 mm long; tepals equal or subequal, erect, densely covered with smooth, appressed whitish hairs, smooth on both faces; fertile stamens with trapezoidal anthers in whorls I and II and rectangular anthers in whorl III; staminodes sagittate, glabrous or pubescent; ovary ovoid or globose, glabrous. Fruit oblate, 2–3 cm in diameter; peduncles 9–11 mm long, gradually widened toward the receptacle, lenticellate; tepals and stamens persistent.

Endemic to Venezuela, where it is found in the Andes (Lara, Portuguesa, and Trujillo) and in the Cordillera de la Costa (Anzoátegui, Monagas, and Sucre; Map 41). In the park, found on the south slope of Guaramacal; 1,650–1,700.

Ferrer-Pereira (2012) observed that the Venezuelan specimens assigned to *Persea rigens* by Kopp (1966) in her revision of the New World taxa of *Persea* appeared to represent a distinct taxon, which he described as *P. rigens* var. *oblaticarpa* emphasizing the oblate (versus spherical) fruit shape. This variety is restricted to South America (Venezuela) whereas the nominate one is found only in Central America (Costa Rica and Panama).

### *Persea* sp. A

Trees, 5–10 m tall; branches terete, striate, glabrous; apical buds elongated and densely covered with yellowish, appressed hairs. Leaves ovate to elliptic, 10–15 × 3.5–5 cm, base obtuse and attenuating shortly on the petiole, margin entire, apex acute, sometimes acuminate, glabrous, secondary veins 10–14 each side of the midrib, diverging from the midrib at an angle ≤ 15–20°, the midrib above impressed to the middle of the blade, rugose, veins raised below; petioles 2–3.5 cm long, caniculate. Flowers and fruit unknown.

This taxon is known from three sterile collections (*Cuello et al. 1953*, *1963*, and *2472*) made in cloud forest on both slopes of Guaramacal National Park in Venezuela (Trujillo; Map 42); 2,500–2,600 m.

Ferrer-Pereira (2012) treated these three Guaramacal collections as representatives of an imperfectly known species related to *Persea hexanthera* L. E. Kopp and/or *P. fendleri* van der Werff.

## *Pleurothyrium* Nees

*Pleurothyrium* Nees, in Lindley, Nat. Syst. Bot., ed. 2, 349, 442. 1836.

Trees or shrubs; twigs solid, rarely hollow and inhabited by ants (not our species). Leaves alternate or clustered at the tip of branchlets, penninerved; domatia absent. Inflorescences in axils of cataphylls, rarely in axils of leaves, thyrso-paniculate (rarely racemose), ultimate divisions cymose, lateral flowers in cymes always opposite. Flowers bisexual; tepals 6 equal or subequal, when subequal inner 3 slightly narrower and shorter; fertile stamens 9, 4-locular (rarely 2-locular); external 6 stamens with anthers curved or bent inward, inner 3 stamens with anthers curved outward; staminodes usually present, inconspicuous; staminal glands conspicuous; pistil generally immersed in receptacle. Fruit a 1-seeded drupe borne on a large cupule; cupule warty or lenticellate; tepals not persisting.

A Neotropical genus found in Central America and South America (Colombia, Venezuela, Suriname, Ecuador, Peru, Bolivia, and Brazil). There are ~50 species of which four are known from Venezuela.

REFERENCE. Van der Werff (1993).

*Pleurothyrium* can be confused with *Nectandra* and *Ocotea*. In *Pleurothyrium*, however, the outer 6 stamens have at least 2 anther cells in a lateral position and all 6 staminal glands are enlarged and grow outward between the 6 external stamens.

**MAP 41.** Distribution of *Persea rigens* var. *oblaticarpa*.

**MAP 42.** Distribution of *Persea* sp. A.

In many species, the staminal glands form a large pillow-like mass with the anthers embedded in the surface (van der Werff, 1993). Inflorescences arising from the axils of cataphylls (and atypical leaves) is another character setting *Pleurothyrium* apart from *Nectandra* and *Ocotea*. Finally, *Pleurothyrium* species have large, distinctly warty cupules, larger than those of *Nectandra* and *Ocotea* and similar to those of *Aniba*.

The results of a molecular study by Penagos Zuloaga et al. (2021) support the monophyly of *Pleurothyrium*, which is sister to *Nectandra* s.str. The clade that contains these genera is part of an early-diverging lineage that also includes *Damburneya*, *Endlicheria*, and most species of *Ocotea*.

***Pleurothyrium costanense*** van der Werff, Ann. Missouri Bot. Gard. 74: 408, fig. 4. 1987.

*Ocotea macropoda* auct., non (Kunth) Mez; Dorr et al., Contr. U.S. Natl. Herb. 40: 104. 2000 [2001].

Trees, 2–20 m tall. Young branches terete to somewhat angled in cross-section, solid; apical buds densely ferruginous pubescent. Leaves elliptic to elliptic-lanceolate, 20–35 × 10–15 cm, base acute, margin plane, very slightly revolute, apex acute or acuminate with tips to 3.5 cm long, 12–16(–20) secondary veins ascending at 40–50° angles to the midrib, anastomosing near the margin; primary and secondary veins prominent below, almost always appressed pubescent, midrib alone impressed above, the secondary veins smooth or sometimes slightly raised, upper surface glabrous; petioles sheathing, widened at the base, 2–3 × 0.4–0.5 cm, ferruginous-pubescent. Inflorescences axillary in foliage leaves or cataphylls, ~10–20 cm long, ferruginous-pubescent, laxly flowered. Flowers whitish, ~1 cm in diam; tepals 6, equal, spreading at anthesis, outer 3 tepals papillose inside and ferruginous-pubescent outside, inner 3 tepals papillose inside and puberulous outside, ~4 mm long; stamens 9, all 4-locular, inner 3 with extrorse cells, outer 6 with lower cells lateral and upper cells introrse; staminal glands conspicuous; style short, stout, and pubescent (easily visible above the androecium); stigma flat, glabrous; ovary glabrous except for 6 longitudinal lines of hairs. Cupules large, distinctly warty.

Endemic to Venezuela where it is found in the Andes (Mérida, Portuguesa, and Trujillo), the Cordillera de la Costa (Anzoátegui, Distrito Capital, Miranda, Monagas, and Sucre), and the Sierra de San Luis (Falcón; Map 43). Our records are from cloud forest on the north slope of Guaramacal; 1,650–1,850 m.

The wood is fragrant.

**MAP 43.** Distribution of *Pleurothyrium costanense*.

## MAGNOLIACEAE

S. MIGUEL NIÑO AND L. J. DORR

Deciduous or evergreen trees or shrubs; leaves and young stems usually with an indumentum of simple hairs. Leaves alternate, distichous, or spiraled, simple, entire or lobed (*Liriodendron*), pinnately veined, coriaceous; petiolate; stipulate, stipules (cataphylls) deciduous, forming annular scars around nodes. Inflorescence bracts (1–)2–11, spathaceous. Flowers almost always solitary, terminal or rarely axillary or pseudolateral, bisexual or rarely unisexual, actinomorphic, pedunculate; sepals and petals not well-differentiated (i.e., sepals petaloid), spirally arranged; sepals 3; petals (5–)6–9; stamens numerous, free, in 3–6 spirally arranged series; filaments short and thick, scarcely differentiated from the anthers; anthers introrse, latrorse, or extrorse, longitudinally dehiscent, connective often distally appendaged; pistils numerous (5–20), superior, spirally arranged on an elongated receptacle, sessile or stipitate, usually free; 1-locular; placentation marginal, placenta 1; ovules 1–2 (sometimes numerous); style simple, terminal; stigma terminal or decurrent. Fruit apocarpic or syncarpic, often an aggregate of follicles, longitudinally dehiscent (*Magnolia*) or indehiscent and samaroid (*Liriodendron*); seed 1 (or more) per carpel, sarcotesta orange or reddish.

A temperate and tropical family found in North America (USA), Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia, Brazil, and Paraguay), and Asia. The family comprises two genera and ~225 species. *Liriodendron* L. has only two species, one each in North America and Asia, while *Magnolia* L. s.l. has ~223 species with the same geographical distribution as the family. Only *Magnolia* is native to Venezuela.

REFERENCES. Wood (1958); Lozano-Contreras (1983); Lozano-C. (1990); Nooteboom (1993, 1998); Azuma et al. (1999, 2001, 2011); Shi et al. (2000); Kim et al. (2001); Wang et al. (2006); Nie et al. (2008).

### *Magnolia* L.

*Magnolia* L., Sp. Pl. 535. 1753.
*Michelia* L., Sp. Pl. 536. 1753.

*Talauma* A. Juss., Gen. Pl. 281. 1789. *Magnolia* sect. *Talauma* (A. Juss.) Baill., Adansonia 7: 3, 66. 1866.
*Manglietia* Blume, Verh. Batav. Genootsch. Kunst. 9: 149. 1823.
*Pachylarnax* Dandy, Bull. Misc. Inform. Kew 1927: 259, 260. 1927.
*Elmerrillia* Dandy, Bull. Misc. Inform. Kew 1927: 260, 261. 1927.
*Kmeria* (Pierre) Dandy, Bull. Misc. Inform. Kew 1927: 260, 262. 1927. *Magnolia* subgen. *Kmeria* Pierre, Fl. Forest. Cochinch. 1: sub t. 1. 1880.
*Dugandiodendron* Lozano, Caldasia 11: 33. 1975. *Magnolia* subsect. *Dugandiodendron* (Lozano) Figlar & Noot., Blumea 49: 90. 2004.

Trees or shrubs; young branches lenticellate; internodes with annular scars formed by deciduous stipules (cataphylls). Leaves almost always shiny above, coriaceous; petioles glabrous or pubescent; stipules free or fused to the petiole. Flowers solitary, terminal, bisexual, initially subtended by spathaceous bracts; stamens numerous, acuminate, flat; gynoecium sessile or shortly pedicellate; carpels numerous or few, free; ovules 2(4–5). Folicules separate, persistent.

A genus of ~223 species of which ~158 species are found in the Americas. The world-wide distribution of the genus includes North America (USA), Central America, the West Indies, South America (Colombia, Venezuela, Guyana, Eucador, Peru, Bolivia, and Brazil), and Asia. Three species are endemic to Venezuela, two of them confined to the Venezuelan Guayana.

REFERENCES. Lozano-C. (1990); Lozano-Contreras (1994); Figlar and Nooteboom (2004).

We follow Figlar and Nooteboom (2004; see also Stevens, 2024) in recognizing a broadly construed *Magnolia*. Our somewhat extensive generic synonymy accounts for the many genera, mostly Asian, recognized earlier by Nooteboom (1993) and/or Frodin and Govaerts (1996) in their reviews of the family. As summarized by Stevens (2024), while molecular data (e.g., Azuma et al., 1999, 2001, 2011; Shi et al., 2000; Kim et al., 2001; Wang et al., 2006; Nie et al., 2008) reveal 11 monophyletic clades within *Magnolia*, support along the backbone of the *Magnolia* phylogeny is poor.

Many North American and Asian species of *Magnolia* are cultivated, including *M. grandiflora* L. native to the southeastern USA, which is sometimes grown in Venezuelan gardens especially ones situated where the local climate is more temperate.

***Magnolia venezuelensis*** (Lozano) Govaerts, in Frodin and Govaerts, World Checkl. Bibliogr. Magnoliaceae 72. 1996. *Talauma venezuelensis* Lozano, Revista Acad. Colomb. Ci. Exact. 17: 781, fig. 3. 1990; Dorr et al., Contr. U.S. Natl. Herb. 40: 107. 2000 [2001].

Trees, 2–4(–20) m tall; branches terete, glabrous; internodes 3.5–5.5 cm long. Leaves alternate, ovate (or juvenile foliage narrowly elliptic), 15–30 × 8–12 cm, base ± truncate (or juvenile foliage cuneate), margin entire, apex acute to obtuse, 6–12 secondary veins each side of the midrib, midrib and secondary veins impressed above, prominent below; petioles 6–12 cm long, thickened basally, glabrous. Inflorescence bracts 3, sheathing the perianth. Flowers solitary, terminal; sepals 3, widely ovate; petals 8, strap-shaped or spathulate; stamens in 3 linear series, connective acute; gynoecium (only known in bud) ellipsoid, 11-carpellate. Fruit unknown.

Restricted to South America (Colombia and Venezuela). In Venezuela, known from the Andes (Lara and Portuguesa) and the Cordillera de la Costa (Distrito Capital; Map 44). Found on the south slope of Guaramacal near La Divisoria de la Concepción; 1,500 m.

This is an infrequently collected and poorly known species (see also Cogollo-Pacheco et al., 2019). Our material, which is sterile and appears to consist of juvenile foliage, resembles the type in its distinctive stipular scars. The type was collected ~50 km to the northeast of Guaramacal in Humocaro Alto (Lara state).

This species was also reported from Delta Amacuro by Thien (2008), but we have been unable to verify the source of his report and therefore do not include this state in our distributional summary or map. Furthermore, *Magnolia venezuelensis* was not included in the flora of the Venezuelan Guayana (Berry et al., 2001), which only treated two endemic species of *Dugandiodendron* (=*Magnolia*).

## MONIMIACEAE

S. MIGUEL NIÑO AND L. J. DORR

Monoecious or dioecious trees, shrubs, or rarely lianas; evergreen; sometimes scandent or semiscandent; usually aromatic. Leaves simple, decussate or in whorls of 3–4, paired leaves often unequal in size, glabrous or pubescent with simple or stellate hairs, oil cells present and appearing as translucent spots; petiolate; estipulate. Inflorescences axillary, cauliflorous, cymose, fasciculate or rarely flowers solitary. Flowers radial, unisexual or rarely bisexual; receptacle (floral cup) well-developed, subglobose or cup-shaped; tepals 3 to many, tepals petaloid, sepaloid,

**MAP 44.** Distribution of *Magnolia venezuelensis*.

or connate and then forming a calyptra; stamens few to many, irregularly arranged in the floral cup; filaments ligulate, usually without appendages; anthers dehiscing by slits or valves; carpels 1–many, free or immersed in the receptacle; stigmas and/or styles free or joined by mucilage plugs; ovules solitary. Fruiting receptacle repand with few to many sessile or stipitate drupes, or drupes enclosed in a fleshy receptacle and exposed at maturity when the receptacle splits.

A family of 28 genera and ~200 species found in Mexico, Central America, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Chile, Paraguay, and Argentina), Africa, Madagascar, Australia, and the Pacific Islands. Only the genus *Mollinedia* Ruiz & Pav. occurs in Venezuela.

REFERENCES. Philipson (1993); Renner et al. (2010).

### *Mollinedia* Ruiz & Pav.

*Mollinedia* Ruiz & Pav., Fl. Peruv. Prodr. 83. 1784.

Dioecious trees or scrambling shrubs; glabrous or pubescent with simple hairs; usually aromatic. Leaves decussate or in whorls of 3; margin of leaf blade dentate, rarely entire. Inflorescences axillary, fasciculate cymes or flowers solitary. Flowers almost always actinomorphic, subtended by small bracteoles; pedicellate. Staminate flowers: tepals 4, subequal; stamens 8–60, dispersed in the floral cup, sessile or with very short filaments; anthers bithecal. Pistillate flowers: tepals connate; carpels 10–50, free on the receptacle; styles very short; stigmas puncatate. Fruiting receptacle almost always pubescent, fleshy, red or orange, turning shiny black when ripe; druplets sessile or pedunculate; seed 1 per druplet.

A Neotropical genus of ~20(90?) species found in Mexico, Central America, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil). Five species occur in Venezuela, three of them in the Andes.

REFERENCES. Perkins (1900); Peixoto (1987).

***Mollinedia ovata*** Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 143. 1798; Berry and Peixoto, in Berry et al., Fl. Venez. Guayana 6: 690–691, fig. 573. 2001; Duno de Stefano, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 589, 591, t. 177c. 2007.

*Mollinedia laurina* Tul., Ann. Sci. Nat., Bot., sér. 4, 3: 43. 1855.

Shrubs or small trees, 3–15(–25) m tall; branchlets and leaf blades below finely pubescent to glabrescent. Leaf blades elliptic, broadly elliptic, ovate, or narrowly oblong, 10–20(–30) × 6–15 cm, base acute, obtuse, or rounded, margin entire or distinctly toothed, apex acute to acuminate, apical tip 1–1.5 cm long, 4–9(–12) secondary veins each side of the midrib, arcuate, chartaceous or coriaceous. Fruiting receptacle repand, greenish orange; drupes sessile, ellipsoidal, green (when fresh) and turning orange or red and finally black (when mature).

South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil). In Venezuela, known from the Andes (Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Sucre and Yaracuy), the Venezuelan llanos (Barinas), and the Venezuelan Guayana (Amazonas and Bolívar; Map 45). Our records are from cloud forest at lower elevations on the south slope of Guaramacal, including collections made near La Divisoria de la Concepción and in the karst area above the Río Amarillo; (1,200–)1,550 m.

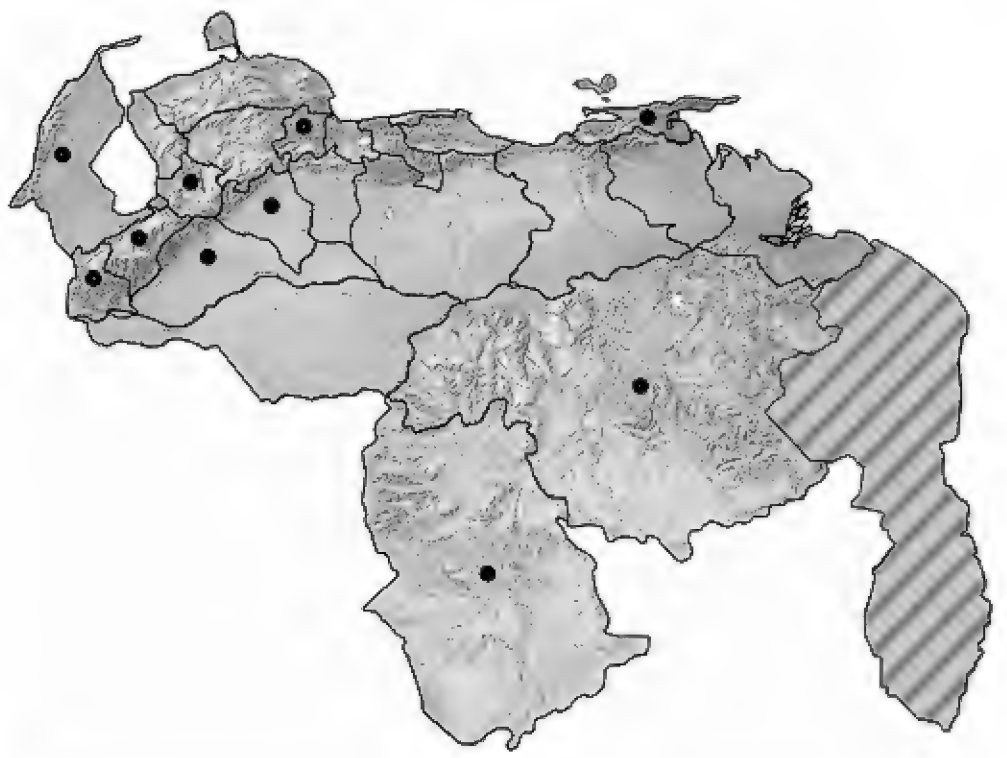
*Mollinedia humboldtiana* Aymard, known from a single staminate collection made ~20 km northwest of Guaramacal, is easily distinguished from our species by its much smaller leaves (3–7 versus 9–13 cm long) and its discretely (versus conspicuously) dentate leaf margin.

## PIPERACEAE

S. MIGUEL NIÑO AND L. J. DORR

Dioecious, monoecious, or hermaphroditic herbs, lianas, shrubs, or trees; terrestrial, saxicolous, or epiphytic; erect, climbing, or decumbent; sometimes succulent. Leaves simple, alternate, opposite, or verticillate (whorled), often succulent, sometimes basal, aromatic, pubescent or glabrous; petiolate or sessile; stipulate. Inflorescences a spike or raceme comprised of umbellate or paniculate spikes, axillary, terminal, or leaf opposed. Flowers bisexual, numerous, generally tightly clustered in a spiral or ring, perianth absent, subtended by a single bract, bracts variable in appearance or shape; stamens 1–6, free or emerging near the base of the ovary; anthers 1–4-locular, laterally dehiscent; ovary superior, sessile or sometimes stipitate, 1-locular with a basal ovule; stigmas 1–5, sessile or shortly elongated. Fruit a dry or fleshy drupe; seed 1.

Piperaceae are found throughout the tropics and subtropics worldwide, including North America (USA), Mexico,



**MAP 45.** Distribution of *Mollinedia ovata.*

Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Chile, Paraguay, Argentina, and Uruguay), Africa, Madagascar, Asia, Australia, and the Pacific Islands. The family includes five genera and ~3,000–3,600 species. Three genera and ~272 species (~82 endemic) are found in Venezuela.

REFERENCES. Trelease and Yuncker (1950); Steyermark (1984); Bornstein (1991); Tebbs (1993a); Jaramillo et al. (2004); Wanke et al. (2007).

## KEY TO THE GENERA OF PIPERACEAE

1a. Herbs; leaves alternate, opposite, or whorled; stamens 2; stigma 1. . . . . ***Peperomia***
1b. Shrubs (sometimes scandent), small trees, or lianas; leaves alternate; stamens 2–6; stigmas 2–5. . . . . 2
  2a. Shrubs (sometimes scandent) or small trees; glabrous or pubescent; inflorescences a solitary spike or raceme, sometimes a compound umbel of spikes . . . . . ***Piper***
  2b. Lianas; glabrous; inflorescences a solitary or paired spike . . . . . ***Manekia***

## ***Manekia* Trel.**

*Manekia* Trel., Repert. Spec. Nov. Regni Veg. 23: 313. [20 Mar] 1927.
*Sarcorhachis* Trel., Contr. U.S. Natl. Herb. 26: 17. [21 May] 1927.

Lianas (herbaceous), climbing or trailing, rooting at nodes; hermaphroditic; stems glabrous, rarely pubescent, with dark brown to black pellucid dots occasionally visible, often succulent. Leaves alternate, entire, venation palmate, with 5–9(–11) primary veins, pellucid dots visible above and/or below (in dried material), or apparently absent; petioles glabrous, sheathing the stem, vaginate entire length with wing-like marginal tissue extending onto or stopping below leaf blade, marginal tissue caducous. Inflorescences spicate, spikes solitary or 2 together, appearing axillary or terminal, erect at anthesis, usually pendulous in fruit; peduncles glabrous to pubescent near rachis attachment, bracteate; rachis fleshy, glabrous or pubescent; floral bracts triangular to rounded-triangular (viewed from above), ciliate, rarely glabrous. Flowers sessile, densely grouped along the rachis, partially immersed in the fleshy axis, never forming bands around the spike; stamens 4; anthers 2-locular. Ovary with 2–5 sessile stigma lobes. Fruit obovoid, glabrous, laterally compressed, completely embedded in rachis.

A genus of three or four species found in Central America, the West Indies, and South America (Colombia, Venezuela, possibly French Guiana, Ecuador, Peru, and Brazil). In South America, *Manekia* has a disjunct distribution; one species is found in the Andes and one in coastal Brazil. The Andean species occurs in Venezuela.

REFERENCES. Steyermark (1971); Schubert et al. (2012); Silva-Sierra and Callejas-Posada (2017).

The relationship between *Manekia* and the unispecific *Zippelia* Blume merits further investigation. The latter genus known only from Indonesia and Malesia has fruit with glochidiate hairs, a character otherwise unknown in the family (Tebbs, 1993a). Nonetheless, molecular data (Wanke et al., 2007) indicate that *Zippelia* is sister to *Manekia* or arguably part of the same clade or even genus.

***Manekia incurva*** (Sieber ex Schult.) T. Arias et al., Novon 16: 206. 2006. *Piper incurvum* Sieber ex Schult., Mantissa 1: 238. 1822. *Sacorhachis incurva* (Sieber ex Schult.) Trel., Contr. U.S. Natl. Herb. 26(2): 17. 1927.

*Sarcorhachis venezuelana* Steyerm., Pittieria 3: 33, fig. 1971; Steyermark, Fl. Venez. 2(2): 606–608, fig. 95, A2 ["A1"], B2, C2, D2. 1984; Ortega et al., BioLlania 5: 53. 1987; Bono, Fl. Veg. Táchira 745. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 125. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 380. 2010. *Manekia venezuelana* (Steyerm.) T. Arias et al., Novon 16: 207. 2006.

Climbing or creeping herbs or lianas; glabrous; branches and leaves fragrant; prophylls 0.2–3 cm long. Leaf blades symmetrical or slightly asymmetrical, ovate to broadly ovate, 5–14 × 4–12 cm, base cordiform to truncate, apex acute or acuminate, dark green above, silvery-green below, veins sulcate or impressed above, elevated below; petioles 2–4(–8) cm long, sheathing. Inflorescences appearing axillary or terminal, spikes 5–10 cm long, usually 2 spikes arising from the same node, spikes initially erect, becoming pendulous, light green or white; peduncles 0.8–1.5 cm long. Fruit ~2–4 mm long.

Found in Central America, the West Indies (Lesser Antilles), and South America (Colombia, Venezuela, possibly French Guiana, Ecuador, and Peru). In Venezuela, known from the Andes (Lara, Portuguesa, Táchira, and Trujillo) and the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Distrito Capital, Falcón, Miranda, Monagas, Sucre, and Yaracuy; Map 46). Park records are from the vicinity of the Laguna de Aguas Negras and from Qda. Honda; 1,700–1,900 m.

Schubert et al. (2012) adopted a broad circumscription of *Manekia incurva*, which is followed here. Their analyses, molecular and morphological, did not allow for clear separation of the four species in the *M. incurva* complex, including *M. venezuelana*. Consequently, Schubert et al. (2012) recognized only three species: a widespread *M. incurva* occurring in Central America, the West Indies (Lesser Antilles), and South America; a species endemic to Haiti; and a species restricted to southeastern Brazil. Silva-Sierra and Callejas-Posada (2017), however, argued that *M. venezuelana* was distinct from the other members of the *M. incurva* complex and endemic to Venezuela. Altogether Silva-Sierra and Callejas-Posada (2017) recognized seven species of *Manekia*.

MAP 46. Distribution of *Manekia incurva*.

## *Peperomia* Ruiz & Pav.

*Peperomia* Ruiz & Pav., Fl. Peruv. Prodr. 8. 1794.

Hermaphroditic herbs; epiphytic, terrestrial, or saxicolous; stems prostrate, erect or decumbent; often succulent. Leaves alternate, opposite, or whorled (verticillate), entire, sometimes peltate, succulent, coriaceous or membranaceous; usually petiolate. Inflorescences simple or compound with numerous spikes. Flowers numerous, sessile; floral bracts orbicular, peltate, glabrous or fimbriate; stamens 2; anthers 2-locular; filaments almost always shorter than the anthers; stigma 1, simple, usually fimbriate, apical or subapical. Fruit a drupe, globose, ovoid, or ellipsoid, sessile or stipitate.

A pantropical (and subtropical) genus of ~1,400–1,600 species found in North America (USA), Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Chile, Paraguay, Argentina, and Uruguay), Africa, Madagascar, Asia, and the Pacific Islands. Most species are Neotropical and ~127 species are found in Venezuela, the majority in mountainous areas.

References. Mathieu and Callejas Posada (2006); Wanke et al. (2006, 2007); Mathieu (2007, 2024); Samain et al. (2009, 2010); Frenzke et al. (2015).

Despite its size, the genus *Peperomia* appears to be monophyletic. *Verhuellia* Miq. is sometimes placed in synonymy under *Peperomia* (see e.g., Tebbs, 1993a), but molecular data indicate that this species-poor genus native to the West Indies (Hispaniola) forms a distinct clade sister to all other Piperaceae (Wanke et al., 2007; Samain et al., 2008). Morphologically, *Verhuelllia* can be distinguished from *Peperomia* by its 4-locular and latrorsely dehiscent (versus 2-locular and extrorsely dehiscent) stamens and by its 3 or 4 (versus 1 or 2) stigmas.

### KEY TO THE SPECIES OF *PEPEROMIA*

1a. Leaves peltate (sometimes only basal leaves peltate) . . . . . 2
  2a. Leaves shortly peltate; petioles inserted 1–3 mm above base of leaf blade; almost always epiphytes or hemiepiphytes (sometimes saxicolous or terrestrial) . . . . . 3
    3a. Leaves ovate, elliptic-ovate, or elliptic-lanceolate, base rounded-cordate; petioles and veins of the leaves glabrous or minutely puberulent, never villous . . . . . ***P. fundacionensis***
    3b. Leaves orbicular-ovate or elliptic-ovate, base rounded; petioles and veins of the leaves sparsely to densely villous . . . . . ***P. peltoidea***
  2b. Leaves distinctly peltate; petioles inserted ≥ 2 mm above base of leaf blade; terrestrial or saxicolous . . . . . 4
    4a. Leaves uneven in size and shape on the same axis, glabrous; leaf blades palmatinerved, 1–7 cm long . . . . . ***P. caraboboensis***
    4b. Leaves uniform in size and shape, pubescent; leaf blades pinnatinerved, 7–30 cm long . . . . . ***P. maculosa***
1b. Leaves not peltate . . . . . 5
  5a. Leaves opposite (sometimes opposite or alternate on same plant) or verticillate . . . . . 6
    6a. Leaves opposite (sometimes opposite or alternate on same plant) or 3(4)-verticillate . . . . . 7
      7a. Stems and leaves sparingly to densely pubescent; inflorescences 1(2–3) per node, terminal or axillary . . . . . ***P. rotundata***
      7b. Stems and leaves glabrous or minutely tomentose-pubescent; inflorescences 1–2 per node, terminal . . . . . ***P.* sp. B**
    6b. Leaves verticillate, some leaves occasionally opposite on the same twig . . . . . 8
      8a. Leaves 3(4)-verticillate, sometimes opposite in terminal branches; leaf blades 2–10 cm long . . . . . 9
        9a. Stems 20–50 cm tall; petioles sheathing and hugging the stem basally, 0.5–1.3 cm long; leaf blades 2.5–8.5(–10) cm long; inflorescences 3–4 axillary or terminal spikes . . . . . ***P. rhexiifolia***
        9b. Stems 5–25 cm tall; petioles not sheathing, 1.5–5 cm long; leaf blades 3–5.5 cm long; inflorescences a solitary terminal spike . . . . . ***P. portuguesensis***
      8b. Leaves 3–8-verticillate, never opposite; leaf blades 0.3–3.5(–4) cm long . . . . . 10

10a. Epiphytic herbs; stems 0.2–0.4 mm thick; leaves 4–8-verticillate; leaf blades 0.3–0.7 cm long; spikes filiform, 0.2–0.4 mm thick . . . . . *P. trichopus*
10b. Epiphytic, saxicolous, or terrestrial herbs; stems 0.4–2 mm thick; leaves usually 4-verticillate; leaf blades 0.5–3.5(–4) cm long; spikes 0.5–1.5 mm thick . . . . . 11
11a. Leaves obovate to spathulate, apex emarginate or twice cleft . . . . . *P. quadrifolia*
11b. Leaves variously shaped (never obovate), apex entire . . . . . 12
12a. Climbing herbs; stems 15–20 cm long, ascending; leaf blades rhomboid, margin ± sinuate . . . . . *P. rhombea*
12b. Epiphytic, saxicolous, or terrestrial herbs; stems 10–40 cm long, some pendent; leaf blades rhomboid, sometimes elliptic, margin generally entire . . . . . 13
13a. Epiphytic herbs, sometimes pendent; leaf apex not ciliate pubescent . . . . . *P. tetraphylla*
13b. Epiphytic, saxicolous, or terrestrial herbs, erect; leaf apex almost always ciliate pubescent . . . . . *P. galioides*
5b. Leaves alternate . . . . . 14
14a. Plants with densely pubescent stems and/or leaves . . . . . 15
15a. Stems glabrous or with scattered hairs; leaf blades densely pubescent; sometimes 2 leaves arising from a single node . . . . . *P. mollisoides*
15b. Entire plant densely pubescent; only 1 leaf arising from a single node . . . . . 16
16a. Epiphytic, saxicolous, or terrestrial herbs; roots at base of erect stems; inflorescences pendent or erect 17
17a. Stems reddish; hairs 1–4 mm long, rigid; inflorescences pendent; floral bracts ovoid or subovoid . . . . . *P. tequendamana*
17b. Stems green (sometimes reddish); hairs 0.2–0.4 mm long; inflorescences erect; floral bracts orbicular-peltate . . . . . *P. trinervula*
16b. Epiphytic or saxicolous herbs; roots at nodes of climbing stems; inflorescences erect . . . . . 18
18a. Hairs on stems 2–4 mm long; some apical leaves appearing opposite; inflorescence peduncles 2.5–5 mm long . . . . . *P. pilicaulis*
18b. Hairs on stems 0.3–0.5 mm long; leaves always alternate; inflorescence peduncles 0.4–1 mm long . . . . . *P. tovariana*
14b. Plants glabrous or with hairs dispersed on leaf edges or at nodes . . . . . 19
19a. Terrestrial, saxicolous, or epiphytic herbs; leaves small, 0.4–2 cm long . . . . . 20
20a. Stems translucent, 10–30 cm tall; petioles 0.3–1.2 cm long; leaves orbicular or rhomboid-orbicular; inflorescence peduncles 1–1.5 mm long; spikes 0.1–2.3 cm long . . . . . *P. hispidula*
20b. Stems not translucent, 5–12 cm tall; petioles 0.1–0.3 cm long; leaves elliptic (some ovate or obovate); inflorescence peduncles 4–15 mm long; spikes 1.5–8 cm long . . . . . *P. tenella*
19b. Epiphytic (sometimes terrestrial) herbs; leaves large, 1.5–15 cm long . . . . . 21
21a. Stems robust, 5–15 mm thick; inflorescences brown or opaque purple, 8–30 cm long, 2–10 mm thick . . . . . *P. adscendens*
21b. Stems not especially robust, 3–5 mm thick; inflorescences green, reddish, or yellowish, 1–20 cm long, 2–4 mm thick . . . . . 22
22a. Inflorescences 2–4, terminal . . . . . 23
23a. Stems decumbent basally, 15–150 cm tall, 4–6 mm thick; leaves pinnatinerved . . . . . 24
24a. Spikes 3–7 in umbellate groups . . . . . *P. talinifolia*
24b. Spikes (1)2, opposite (never umbellate) . . . . . *P. alpina*
23b. Stems erect (not decumbent), 2–25 cm tall, 2–4 mm thick; leaves 2–3-palmatinerved . . . . . 25
25a. Stems angular in cross-section; basal leaves alternate, apical ones almost always opposite; leaves 3–5-palmatinerved . . . . . *P. san-joseana*
25b. Stems terete in cross-section; basal and apical leaves alternate; leaves 2–3-palmati- or plinerved . . . . . *P. glabella*
22b. Inflorescences 1(2), terminal or axillary . . . . . 26
26a. Leaves palmatinerved with 1–3 lateral veins . . . . . 27
27a. Petioles winged, sheathing the stem . . . . . *P. alata*
27b. Petioles sheathing or winged without sheathing the stem . . . . . 28
28a. Terrestrial or epiphytic herbs; leaves 2-palmatinerved, crystalline glands not very evident; spikes 1–8.5 cm long; fruit apex oblique and pointed . . . . . *P. dendrophila*

28b. Epiphytic (rarely saxicolous) herbs; leaves 2–3-palmatinerved, densely black dotted; spikes 6–10(–15) cm long; fruit shortly beaked, beak minute. . . . . *P. glabella*
26b. Leaves pinnatinerved with 3–7 secondary veins each side of the midrib . . . . . 29
29a. Entire living plant very fragrant (with odor of cilantro); leaf apices long acuminate with 2–3 cm long tips . . . . . *P. acuminata*
29b. Entire living plant without fragrance; leaf apices rounded, obtuse or when acuminate with 0.5–1 cm long tips. . . . . 30
30a. Petioles 0.5–1 cm long, winged, surrounding the stem basally . . . . . *P. succulenta*
30b. Petioles 1–10 cm long, not surrounding the stem basally. . . . . 31
31a. Leaves borne along the length of the stem; petioles generally purple; apices of leaf blades obtuse (occasionally emarginate), glabrous; fruit 0.7–1.2 mm long, rostrate, beak 0.2–0.4 mm long . . . . . *P. obtusifolia*
31b. Leaves borne on the distal portion of the stem; petioles green; apex of leaf blades acuminate, almost always ciliate; fruit 0.4–0.7 mm long, not beaked . . . . . *P. petrophila*

***Peperomia acuminata*** Ruiz & Pav., Fl. Peruv. 1: 32, t. 51, fig. a. 1798; Steyermark, Fl. Venez. 2(2): 29–33, fig. 1, A2, B2, C2. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 690. 2003.

*Peperomia acuminata* Ruiz & Pav. f. *rubra* Steyerm., Fl. Venez. 2(2): 33. 1984.

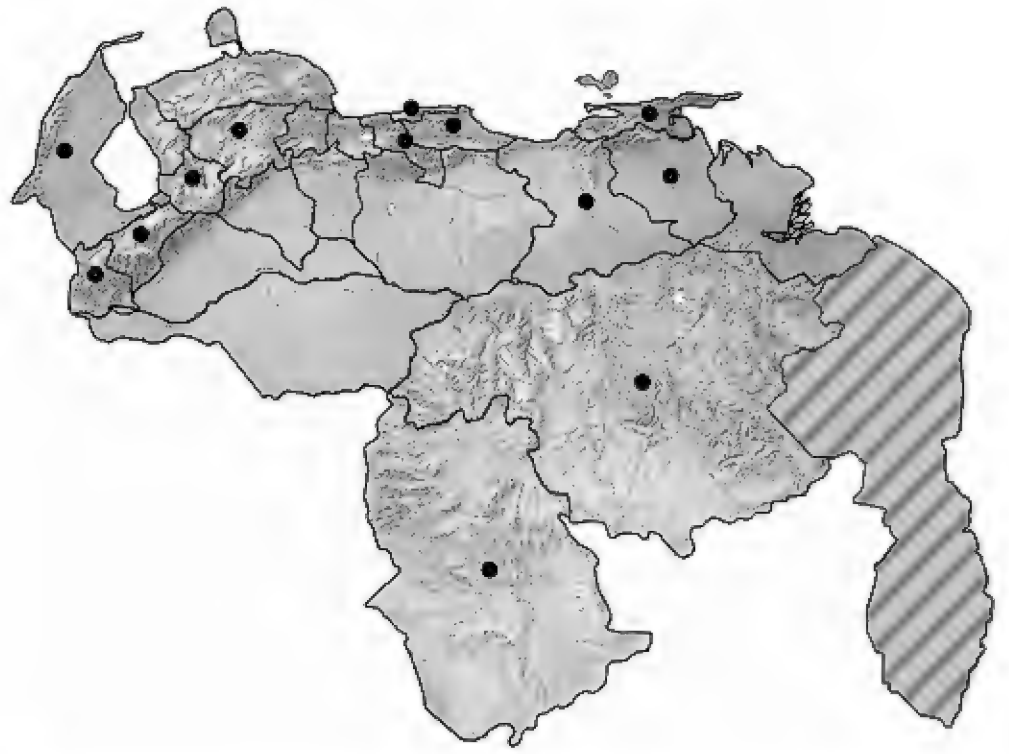
Terrestrial or sometimes epiphytic herbs; stems erect, not branched, to 5.5 cm tall; glabrous; succulent; entire plant very fragrant. Leaves alternate; leaf blades oblanceolate, elliptic, or narrowly lanceolate-elliptic, 1.5–3.5 × 4.5–15 cm, base cuneate, sometimes the lower half of the margin ciliate, apex acute or more commonly acuminate with 2–3 cm long tips, dark green above, silvery-green below, obscurely 4–7-pinnatinerved, membranous (when dry); petioles 0.5–5 cm long, winged. Inflorescences solitary densely-flowered spikes 5–20 cm long, terminal or leaf opposed, erect; peduncles 2–5 cm long. Floral bracts orbicular-peltate, glandular-punctate. Fruit basally attached to the rachis, ovoid or globose, 0.3–0.5 × 0.6–1.2 mm, apex very short, 0.1–0.2 mm long.

Found in Mexico, Central America, the West Indies (Greater Antilles), and South America (Colombia, Venezuela, possibly Guyana, Ecuador, Peru, Bolivia, and Brazil). Widespread in Venezuela, reported from the Andes (Lara, Mérida, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Distrito Capital, Miranda, Monagas, and Sucre), and the Venezuelan Guayana (Amazonas and Bolívar; Map 47). In the park, known from the north slope of Guaramacal and the Fila de Agua Fría; 1,600–2,800(–3,100) m.

COMMON NAME. Cilantro.

USE. This species is edible (fide *Stergios 17617* in sched.). Its fresh leaves and stems are used to flavor food.

*Peperomia acuminata* and *P. adscendens* C. DC. (see key and below) are more easily separated in the field than in the herbarium. The former is a succulent, distally branched herb, with fleshy but often translucent leaves that is found in forest understory. It has a very strong odor of cilantro (*Coriandrum sativum* L.). *Peperomia adscendens* rarely branches distally and its leaves are thicker and opaque. It favors open areas and most notably it does not have a cilantro-like odor. Inflorescences of both *P. acuminata* and *P. adscendens* are erect at anthesis. However, while inflorescences of the former remain erect in fruit, they are reflexed in the latter (Mathieu and Callejas Posada, 2006).



**MAP 47.** Distribution of *Peperomia acuminata*.

***Peperomia adscendens*** C. DC., J. Bot. 4: 140. 1866; Steyermark, Fl. Venez. 2(2): 33–35, fig. 1, A1. 1984.

FIGURE 5A

Epiphytic or hemiepiphytic and sometimes terrestrial herbs; stems up to 50 cm long, 5–15 mm thick, leaf scars conspicuous; glabrous; succulent. Leaves alternate, almost always aggregated in the distal part of the stem; leaf blades widely oblanceolate to elliptic-oblanceolate, 15–30 × 5–12 cm, base attenuate to decurrent, margin not ciliate, apex acute to acuminate, dark green above, light green to silvery below, 5–8 secondary veins each side of the midrib, ascending, midrib raised below; petioles 1–4 cm long, winged. Inflorescences almost always solitary (rarely 2) densely-flowered spikes, 8–30 cm long, 2–10 mm thick, brown or opaque purple, erect or slightly curved (reflexed in fruit), terminal or leaf-opposed. Floral bracts orbicular-peltate. Fruit basally attached to the rachis, globose or oblong-ellipsoid, 0.8–1.1 × 0.5 mm.

Found in Mexico, Central America, and South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, known

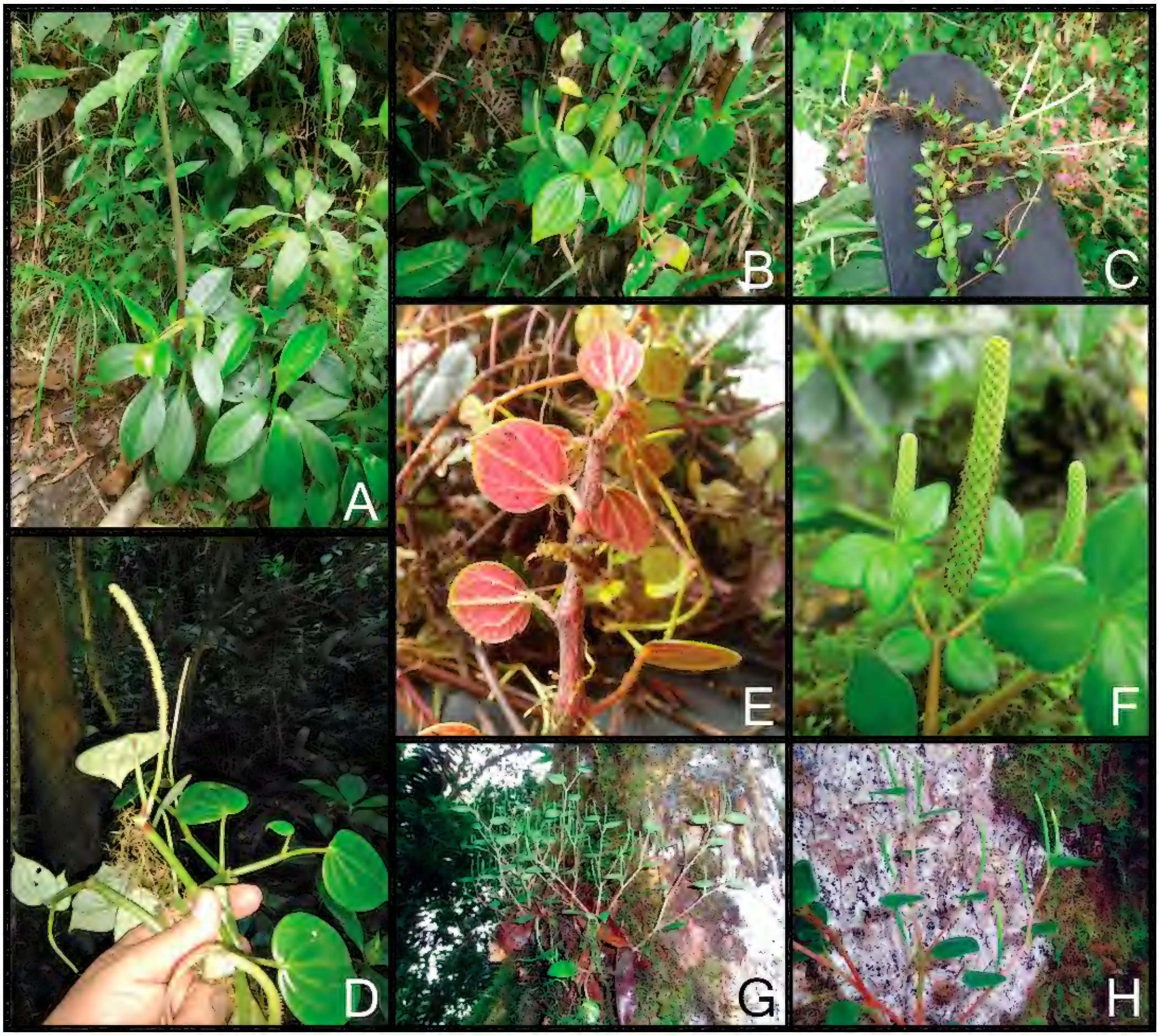


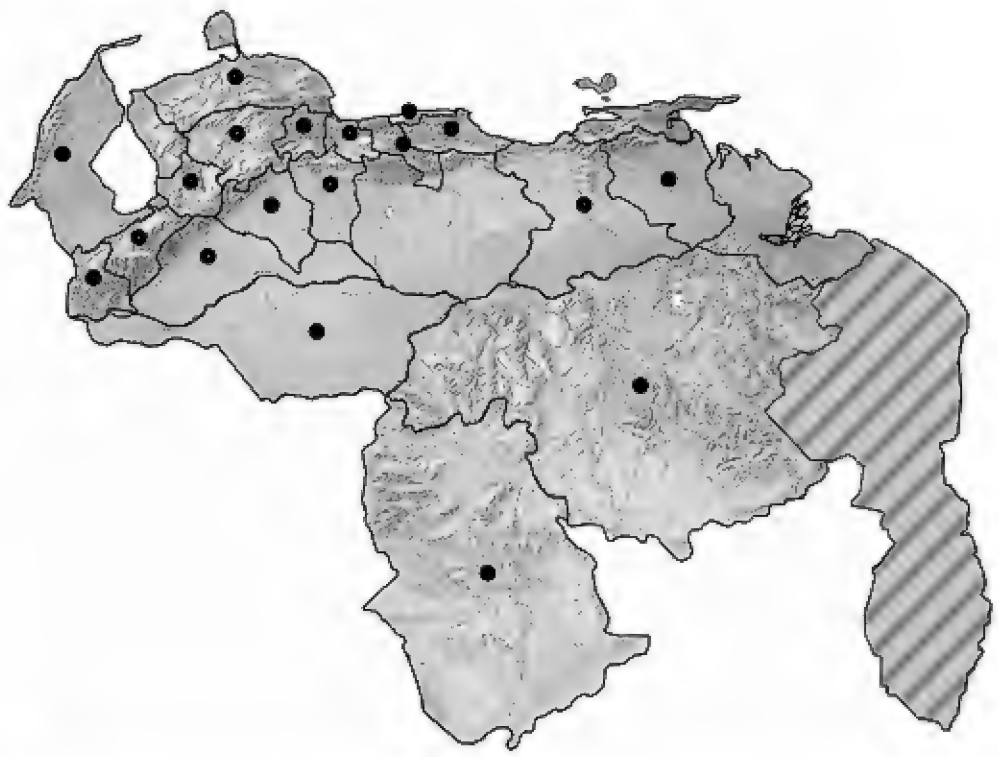

**FIGURE 5. A.** Piperaceae, *Peperomia adscendens* C. DC. Habit and solitary inflorescence. **B.** *P. dendrophila* Schltdl. & Cham. Habit. **C.** *P. galioides* Kunth var. *galioides*. Habit. **D.** *P. peltoidea* Kunth. Habit. **E.** *P. tequendamana* Trel. Leaves below. **F.** *P. tetraphylla* Hook. & Arn. var. *tetraphylla*. Habit and inflorescence. **G, H.** *P. trinervula* C. DC. G. Habit and inflorescence. H. Close-up of inflorescence. (A–H, photographer D. Canelón).

from the Andes (Lara, Mérida, and Trujillo) and the Cordillera de la Costa (Aragua, Distrito Capital, and Sucre; Map 48). In the park, collected on the north slope of Guaramacal along the trail from Agua Fría to the Laguna de Aguas Negras and near the Laguna de los Cedros; 1,900–2,100 m.

*Peperomia adscendens* unlike *P. acuminata* (see key and above) is often epiphytic or hemiepiphytic. It is easily recognized by its robust succulent stems, and inflorescences and leaves with brown or purple spots.

***Peperomia alata*** Ruiz & Pav., Fl. Peruv. 1: 31, t. 48, fig. b. 1798; Steyermark, Fl. Venez. 2(2): 35–39, fig. 3, A2, B2. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 690. 2003.

MAP 48. Distribution of *Peperomia adscendens*.



MAP 49. Distribution of *Peperomia alata*.

Epiphytic, terrestrial, or saxicolous herbs; stems 10–40 cm tall, winged, glabrous, succulent. Leaves alternate, distichous; leaf blades elliptic to broadly elliptic or elliptic-lanceolate, usually widest in the middle, 2–4 × 4–12 cm, base acute, apex long acuminate, deep green above with impressed veins, pale green below, palmati- or plinerved with 3–5 principal veins, membranous (when dry); petioles 0.5–2 cm long, winged, sheathing the stem. Inflorescences simple, spikes solitary or sometimes 2–3 spikes terminating a stem, 5–15 cm long, erect or ascending, terminal, leaf-opposed, or axillary above; peduncles 3–25 mm long. Floral bracts orbicular-peltate, 0.5–0.7 mm in diameter. Fruit sub-basally attached to the rachis, globose or subglobose, 0.5–1 mm in diameter.

North America (USA), Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, and Argentina). Widespread in Venezuela, found in the Andes (Barinas, Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Cojedes, Distrito Capital, Falcón, Miranda, Monagas, and Yaracuy), the Venezuelan llanos (Apure), and the Venezuelan Guyana (Amazonas and Bolívar; Map 49). Park records are from both slopes of Guaramacal, including near La Divisoria de la Concepción and the karst area above the Río Amarillo on the south slope; (~1,200–)1,600–2,100 m.

***Peperomia alpina*** (Sw.) A. Dietr., Sp. Pl., ed. 6, 1: 157. 1831; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 690. 2003. *Piper alpinum* Sw., Prodr. 15. 1788.

*Peperomia longimucronata* C. DC., Notizbl. Bot. Gart. Berlin-Dahlem 6: 497. 1917 ("*longemucronata*"); Steyermark, Fl. Venez. 2(2): 132–133, fig. 18 A1, B1, C1. 1984 ("*longemucronata* f. *longemucronata*").

*Peperomia longirostrata* Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 2: 676. 1950. *Peperomia longimucronata* f. *longirostrata* (Yunck.) Steyerm., Fl. Venez. 2(2): 133. 1984 ("*longemucronata*").

Terrestrial herbs; stems decumbent basally, succulent, 15–35 cm long, 4–5 mm thick in basal branches, glabrous. Leaves alternate; leaf blades ovate, ovate-elliptic to elliptic-obovate, 8–11 × 4–6 cm, base acute, margin glabrous or minutely ciliate, apex acuminate, with a 0.5–1.2 cm long tip, minutely pubescent above especially along midrib, glabrous below, pinnatinerved, secondary veins 4–6 each side of the midrib; petioles winged, deeply channeled (canaliculate) to sheathing, 1.5–4 cm long. Inflorescences terminal, 2(1) spikes, 10–15 cm long, pendulous or ascending; peduncles 3–4 cm long. Floral bracts ovoid, suborbiclar to orbicular, 0.5–0.7 mm in diameter. Fruit basally attached to the rachis, ovoid or cylindrical, 0.8–1 mm long sessile, dispersed, and separate.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Guyana, French Guiana, and Ecuador). Widespread in Venezuela (Anzoátegui, Aragua, Bolívar, Carabobo, Cojedes, Distrito Capital, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Sucre, Táchira, Trujillo, and Yaracuy; Map 50). In the park, collected on the north slope of Guaramacal near Casa Vicuyal; 2,100 m.

***Peperomia caraboboensis*** Steyerm. & G. S. Bunting, Acta Bot. Venez. 6: 81, fig. 1. 1971 [1972]; Steyermark, Fl. Venez. 2(2): 63, 65, 66, fig. 6, A1, B1, C1, D1. 1984.

Terrestrial herbs; stems ~10–30 cm tall, green or with purple spots toward the apex, branched above, erect or decumbent; pubescent; fleshy. Leaves alternate, fleshy or subcoriaceous; basal and lower blades suborbicular-peltate, 2–4 × 1.5–3.5 cm, base rounded or obtuse to subacute, apex rounded or widely acute to subacute, mid-stem and upper blades not peltate, widely suborbicular-ovate, base subcordate, apex subacute to subobtuse, dark green above with silvery-gray stripes, silvery-green below, 5–9-palmately nerved; petioles of basal leaves 5–7 cm long and of apical leaves 1–3 cm long. Inflorescences simple, terminal or axillary; spikes solitary or 2 emerging together, 3–7 cm

**MAP 50.** Distribution of *Peperomia alpina*.

long, curved; peduncles 1–2.5 cm long. Floral bracts orbicular-peltate. Fruit subglobose, ~1 mm long.

Endemic to Venezuela where it is found in the Andes (Portuguesa and Trujillo) and in the Cordillera de la Costa (Carabobo and Distrito Capital; Map 51). In the park, our sole record is from the Laguna de Aguas Negras near Batatal; 2,000 m.

***Peperomia dendrophila*** Schltdl. & Cham., Linnaea 5: 74. 1830; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 691. 2003.

FIGURE 5B

*Peperomia angularis* C. DC., in de Candolle, Prodr. 16(1): 415. 1869; Bono, Fl. Veg. Táchira 731. 1996 ("*angularis* var. *angularis*"); Dorr et al., Contr. U.S. Natl. Herb. 40: 123. 2000 [2001] (as to *Stergios 2567*); Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 370. 2010 (as to *Stergios 2567*).

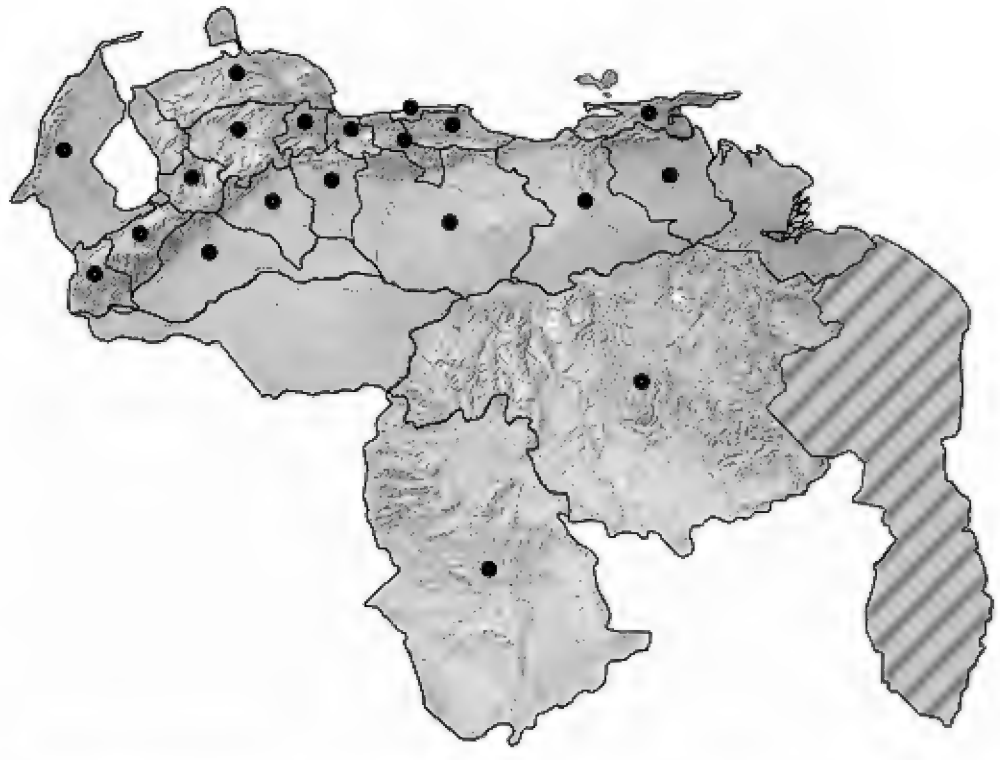
Terrestrial or epiphytic herbs; stems basal, erect or climbing, 3–40 cm long. Leaves alternate, glabrous, variable in shape and size on the same axis, succulent; leaf blades lanceolate-elliptic, widely ovate-elliptic, or oblanceolate, 2–6 × 1.3–3.5 cm, base rounded or decurrent, apex acute or long acuminate, palmately 2-nerved, green or pale-green and veins impressed above, green and veins slightly prominent below; petioles 2–12 cm long, glabrous. Inflorescences simple, terminal or leaf-opposed, spikes solitary or sometimes 2 spikes at the same node, 1–8.5 cm long; peduncles 5–15 mm long, green and brown at maturity. Floral bracts membranous, pellucid-punctate, yellowish; flowers densely clustered on the rachis. Fruit sub-basally attached to the rachis, subglobose or ovoid, generally longer than wide, ~0.9 mm in diameter, apex oblique and pointed.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Ecuador, and Peru). Widespread in Venezuela, occurring in the Andes (Barinas, Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Cojedes, Distrito Capital, Falcón, Guárico, Miranda, Monagas, Sucre, and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 52). In the park, collected in cloud forest on both slopes of Guaramacal, including near La Divisoria de la Concepción; 1,700–2,500 m.

Although Mathieu (2024) restricted *Peperomia dendrophila* to Mexico and Central America, we follow Steyermark and Callejas-Posada (2003), Callejas (2008), Callejas and Patiño (2011), and Bernal (2016) in recognizing this species as being more wide-spread and extending to South America.

Steyermark (1984) appears to have misinterpreted *Peperomia angularis* and although this name is considered a synonym

**MAP 51.** Distribution of *Peperomia caraboboensis*.



**MAP 52.** Distribution of *Peperomia dendrophila*.

of *P. dendrophila* by Callejas (2008), Steyermark's concept agrees with what is recognized here as *P. san-joseana* C. DC. (see below).

***Peperomia fundacionensis*** Steyerm., Fl. Venez. 2(2): 101, fig. 12, A3, B3, [C3]. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 692. 2003.

Epiphytic or hemiepiphytic herbs; stems 15–25 cm long, branched, rooting at most nodes; pellucid-punctate or glabrous; succulent. Leaves alternate; leaf blades variable in shape and size along each branch, ovate, elliptic-ovate to elliptic-lanceolate, 4–5 × 3–4 cm, base rounded-cordate, margin minutely ciliate, apex abruptly acute, minutely puberulent along veins above, obscurely glandular dotted above, more noticeably pellucid-punctate below, 4–9-pli- or palmately-nerved, nerves impressed above and below or the midrib alone raised below, fleshy-subcoriaceous; petioles 3.5–8 cm long, shortly peltate, often inserted 1–2 mm from the blade margin, glabrous. Inflorescences simple, terminal or axillary, spikes 1.5–3.5(–6) cm long, green or white; peduncles 1–3 cm long, minutely puberulent, 1–2-bracteate. Floral bracts suborbicular, membranous, glabrous; flowers loosely clustered on the rachis, sessile. Fruit basally fixed to the rachis, ellipsoid-ovoid, 0.7–1 × 0.4–0.6 mm, smooth, rostrate, beak 0.2–0.3 mm long, erect or curved.

Endemic to Venezuela, where it is known from the Andes (Táchira and Trujillo) and the Serranía Yutajé in the Venezuelan Guayana (Amazonas; Map 53). Collected once in the park on the south slope near the village of Guaramacal; 1,500 m.

***Peperomia galioides*** Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 1: 58, t. 17. 1815 [1816]; ibid. [qu.] 1: 71, t. 17. 1815 [1816]; Steyermark, Fl. Venez. 2(2): 103–106, fig. 13, A3, B3. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 692. 2003. *Peperomia inaequalifolia* var. *galioides* (Kunth) Pino, Avonia 28(2): 45. 2010.

The nominate variety is the only one found in Venezuela.

***Peperomia galioides*** var. ***galioides***

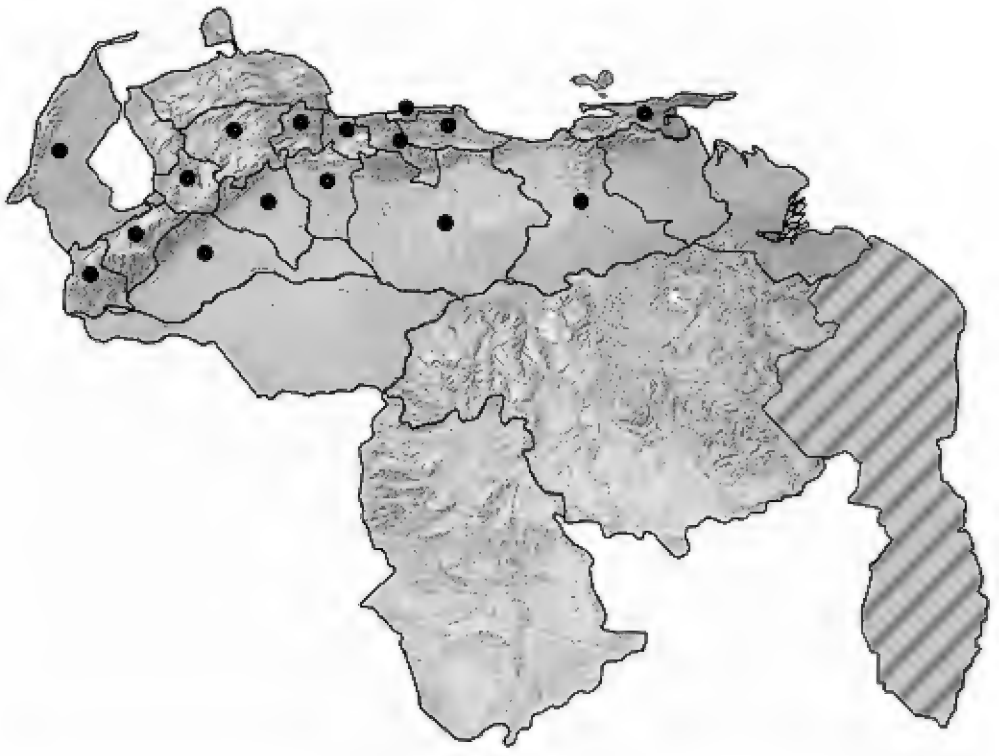
FIGURE 5C

Terrestrial, saxicolous, or epiphytic herbs; stems branching, 10–80 cm tall; caespitose; succulent. Leaves verticillate, 3–6 per node, sometimes solitary, equal or unequal; leaf blades variable in shape, spathulate or ovate to elliptic, 0.5–2.5 × 0.2–0.6 cm, base acute to subacute, apex obtuse or rounded, palmately 3-nerved or with only the midrib visible; petioles 2–4 mm long. Inflorescences simple, terminal or axillary, sometimes 2–4 spikes arising from a single node, spikes 1–8 cm long, green; peduncles 5–15 mm long. Floral bracts orbicular-peltate, 0.5–0.7 mm in diameter. Fruit sub-basally attached to the rachis, globose, 0.5–0.8 mm in diameter, pellucid-punctate, papillate, or verrucose, shortly beaked, beak oblique or prominent.

Found in Mexico, Central America, the West Indies (Greater Antilles), and South America (Colombia, Venezuela, possibly Guyana, Ecuador, including the Galapagos Islands, Peru, Bolivia, and Brazil). Widespread in Venezuela, known from the Andes (Barinas, Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Cojedes, Distrito Capital, Guárico, Miranda, Sucre, and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 54). In the park, found in cloud forest and subpáramo on both slopes of Guaramacal; 1,800–3,100 m.

*Peperomia galioides* var. *aromatica* C. DC. is known only from the type locality in Peru and the principal character distinguishing it from the nominate variety appears to be very weak (i.e., "ramulis desectis in sicco aromaticis" or twigs aromatic when dry).

**MAP 53.** Distribution of *Peperomia fundacionensis*.



**MAP 54.** Distribution of *Peperomia galioides* var. *galioides*.

***Peperomia glabella*** (Sw.) A. Dietr., Sp. Pl., ed. 6, 1: 156. 1831; Steyermark, Fl. Venez. 2(2): 107–110, fig. 13, A1, B1, C1. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 693. 2003; Duno de Stefano and Aymard, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 620. 2007. *Piper glabellum* Sw., Prodr. 16. 1778.

*Peperomia melanostigma* var. *nervulosa* C. DC., in de Candolle, Prodr. 16(1): 409. 1869 ("β, *nervulosa*"). *Peperomia glabella* var. *nervulosa* (C. DC.) Yunck., Ann. Missouri Bot. Gard. 37: 98. 1950; Steyermark, Fl. Venez. 2(2): 107–112. 1984; Bono, Fl. Veg. Táchira 732. 1996; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 691. 2003.

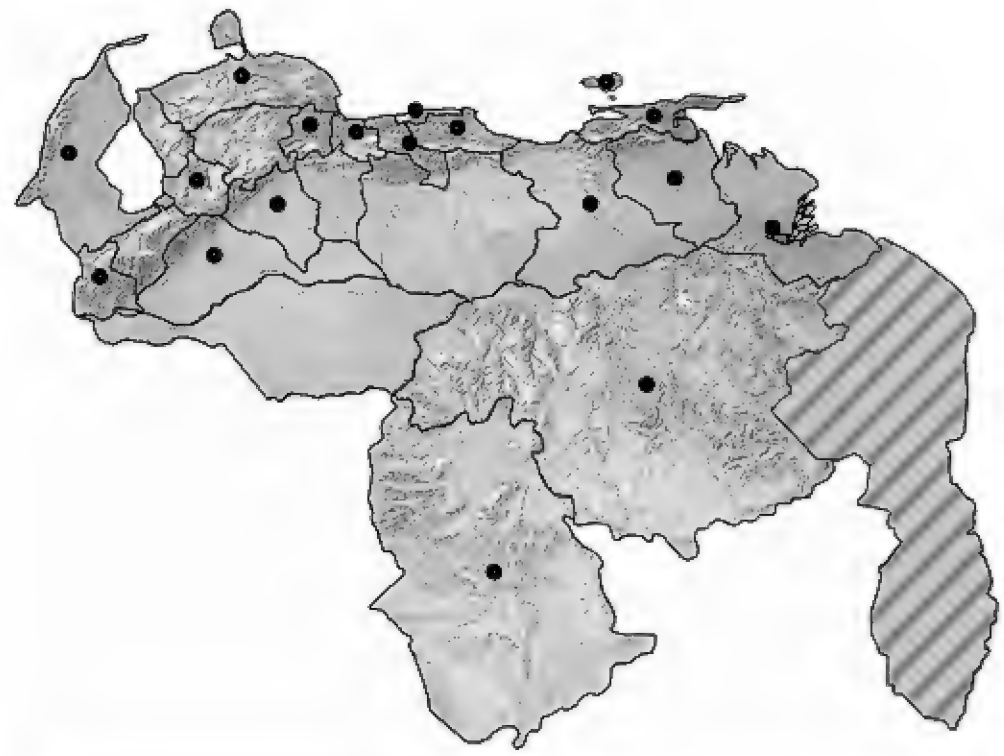
*Peperomia glabella* var. *obtusa* Steyerm., Fl. Venez. 2(2): 112. 1984.

*Peperomia dendrophila* auct., non Schltdl. & Cham.; Dorr et al., Contr. U.S. Natl. Herb. 40: 123. 2000 [2001] (as to *van der Werff et al. 7551*).

Epiphytic (rarely saxicolous) herbs; stems repent, scandent, or erect, 2–20 cm long, generally branched, terete in cross-section, basal nodes with roots; glabrous; sunloving. Leaves alternate; blades generally elliptic to lanceolate, occasionally ovate to obovate, (1.5–)2–6(–8) × 0.5–2.5(–4) cm, base cuneate, apex acuminate, densely black-punctate (when dry), palmati- or plinerved, secondary veins 2–3 each side of the midrib, membranous; petioles 0.4–1.2(–2) cm long, margins ciliate. Inflorescences simple, terminal and axillary, spikes solitary, 6–10(–15) cm long, erect or arched, dark green to reddish; peduncles 0.4–1 cm long, black-dotted (when dry), glabrous. Floral bracts orbicular-peltate; flowers densely clustered on the rachis, sessile. Fruit basally attached to the rachis, globose-ovoid, 0.4–0.6 mm long, shortly beaked, beak minute and oblique, black.

North America (USA), Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil); also introduced in Asia (Peninsular Malaysia). In Venezuela, found in the Andes (Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Distrito Capital, Falcón, Miranda, Monagas, Sucre, and Yaracuy), Nueva Esparta, the Venezuelan llanos (Barinas), and the Venezuelan Guayana (Amazonas, Bolívar, and Delta Amacuro; Map 55). In the park, collected on both slopes of Guaramacal, including the south slope near La Divisoria de la Concepción; 1,500–2,350 m.

*Peperomia glabella* is easily recognized by the numerous black dots that cover all parts of the plant.



**MAP 55.** Distribution of *Peperomia glabella.*

***Peperomia hispidula*** (Sw.) A. Dietr., Sp. Pl., ed. 6, 1: 165. 1831; Steyermark, Fl. Venez. 2(2): 122–124, fig. 16, A4, B4, C4. 1984. *Piper hispidulum* Sw., Prodr. 15. 1788.

The nominate variety is the only one found in Venezuela.

***Peperomia hispidula*** var. ***hispidula***

Terrestrial herbs; stems 10–30 cm tall, translucent; nodes hispidulous. Leaves alternate, sometimes subopposite toward apices of stems; leaf blades orbicular or rhomboid-orbicular, widest toward the base, 0.5–2 × 0.5–2 cm, base truncate, rounded, or subcordate, apex rounded to obtuse, palmately 3–5-nerved, midrib strongly branched at the middle of the blade, dull green above, sometimes with white spots, silvery green below; petioles 0.3–1.2 cm long, minutely hispidulous puberulent near base of leaf blade. Inflorescences simple, terminal or leaf-opposed, spikes solitary, filiform, 0.1–2.3 cm long; peduncles filiform, 1–1.5 mm long. Floral bracts orbicular-peltate, ~3 mm in diameter; flowers scattered and distant on a glabrous rachis. Fruit globose-ovoid, 0.8–1.1 mm long, shortly pedicellate, terminating in a curved, styliform tip, sparingly punctate.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay). In Venezuela, known from the Andes (Lara, Mérida, Táchira, and Trujillo), the Sierra de Perijá (Zulia), and the Cordillera de la Costa (Aragua, Distrito Capital, and Miranda; Map 56). In the park, collected on the north slope of Guaramacal; 2,000–2,400 m.

***Peperomia maculosa*** (L.) Hook., Exot. Fl. 2: t. 92. 1825 [1824]; Steyermark, Fl. Venez. 2(2): 142–144, fig. 19, A3, B3. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 694, fig. 588. 2003. *Piper maculosum* L., Sp. Pl. 30. 1753.

Terrestrial or saxicolous herbs; stems 3–40 cm tall, moderately short-pubescent; succulent. Leaves alternate, 3–5 per plant; leaf blades obovate, rounded to obtuse, uniform in shape and size, 7–30 × 5–12.5 cm, peltate with the petiole attached 2–10 mm from the basal margin of the leaf blade, base subcordate or subtruncate, apex acuminate, pinnatinerved, secondary veins 4–6 each side of the midrib, dark green, succulent; petioles 5–30 cm long, usually densely pilose. Inflorescences simple or compound, terminal or leaf-opposed, spikes 10–30 cm long, pale green with purple; peduncles 2–8 cm long. Fruit basally or subbasally attached to rachis, globose or ellipsoid, 1.3–1.5 mm long, apex curved, 0.8–1.1 × 0.1–0.2 mm.

**MAP 56.** Distribution of *Peperomia hispidula* var. *hispidula*.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia, and Brazil). In Venezuela, *Peperomia maculosa* is found in the Andes (Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Cojedes, Distrito Capital, Falcón, Guárico, Miranda, Monagas, Sucre, and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 57). Our records are from La Divisoria de La Concepción and the south slope of Guaramacal; 1,600–1,700 m.

COMMON NAME. Cilantro.

USE. This species is used to make a hot sauce (fide *Liesner et al. 12906* in sched.).

**MAP 57.** Distribution of *Peperomia maculosa*.

*Peperomia mollisoides* Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 2: 633, fig. 555. 1950; Steyermark, Fl. Venez. 2(2): 158–159, fig. 22, A1, B1, C1. 1984.

Epiphytic herbs or climbers; stems angular in cross-section, rooting at the nodes; glabrous or barely pubescent. Leaves alternate, sometimes 2 arising from the same node; leaf blades ovate or elliptic-ovate, widest in the middle, 1–2 × 0.5–1 cm, base subacute to subobtuse, apex obtuse or slightly acute, densely crispate pubescent above and below, pale green above, silvery green below, palmately 3-nerved; petioles 3–11 mm long, glabrous to imperceptibly papillate. Inflorescences simple, terminal; peduncles 5–20 mm long; spikes 10–20 mm long, green or wine-red to lavender. Fruit sub-basally attached to rachis, globose-ovoid, 0.5–0.6 mm in diameter, minutely verrucose, yellowish-brown.

Found in Andean South America (Colombia, Venezuela, and Ecuador). In Venezuela, known from the Andes (Trujillo), the Sierra de Perijá (Zulia), and the Cordillera de la Costa (Aragua, Carabobo, Distrito Capital, and Monagas; Map 58). In the park, found on the north slope of Guaramacal; 1,600–1,850 m.

*Peperomia obtusifolia* (L.) A. Dietr., Sp. Pl., ed. 6, 1: 154. 1831; Steyermark, Fl. Venez. 2(2): 161–166, fig. 22, A3, B3. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 695, fig. 595. 2003. *Piper obtusifolium* L., Sp. Pl. 30. 1753.

*Peperomia decurrens* auct., non C. DC.; Dorr et al., Contr. U.S. Natl. Herb. 40: 123. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 371. 2010.

The nominate variety is the only one found in Venezuela.

***Peperomia obtusifolia* var. *obtusifolia***

Epiphytic, terrestrial, or sometimes saxicolous herbs; stems erect or straight, stoloniferous, rooted at the lower nodes, green

**MAP 58.** Distribution of *Peperomia mollisoides*.

or with purple spots; glabrous except for the peduncles. Leaves alternate, clustered toward the apex of the plant; leaf blades obovate to rarely elliptical or subspathulate, sometimes lanceolate, 2.5–12(–16) × 1.5–6(–9.5) cm, base narrowly cuneate, apex obtuse, occasionally emarginate, glabrous, dark green above, paler green below, 5–6 secondary veins each side of the midrib, thick-succulent, coriaceous (when dry); petioles 1–10 cm long, not surrounding the stem basally, generally purple. Inflorescences simple, sometimes compound, axillary, leaf-opposed or terminal; peduncles 2–4.5(–10) cm long; spikes 1–3 on a common peduncle, erect or curved, 2–6.5 cm long. Fruit basally attached to rachis, globose, ovoid to ellipsoid, 0.7–1.2 mm long, rostrate, the beak prominent, curved, 0.2–0.4 mm long.

Found in North America (USA), Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil); introduced in the Mariana Islands. In Venezuela, found in the Andes (Lara, Mérida, Táchira, and Trujillo), the Sierra de Perîja (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Miranda, Monagas, Sucre, and Yaracuy), Nueva Esparta, and the Venezuelan Guayana (Amazonas, Bolívar, and Delta Amacuro; Map 59). In the park, found in cloud forest on the south slope near the village of Guaramacal; 1,500 m.

***Peperomia peltoidea*** Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 1: 51, t. 7. 1815 [1816]; ibid. [qu.] 1: 61, t. 7. 1815 [1816]; Steyermark, Fl. Venez. 2(2): 182–186, fig. 25, A1, B1. 1984.

FIGURE 5D

Epiphytic, saxicolous, or occasionally terestrial herbs, often climbing or scandent; stems rooting at the nodes, pubescent. Leaves alternate, uniform in size and shape on the same axis, peltate or shortly peltate; leaf blades orbicular-ovate or elliptic-ovate, 2–10 × 2.5–7.5 cm, base rounded, truncate, or subcordate, margin pilose, apex almost always acuminate, palmately- or plinerved with 5–7 veins, dark green above, silvery green below, ± succulent or fleshy; petioles 2–5(–8) cm long, sparsely to densely villous. Inflorescences simple, terminal or lateral, erect or pendulous; peduncles 1–5 cm long, villous to glabrescent; spikes 3–8(–14) cm long, brown or purple. Floral bracts orbicular-peltate. Fruit basally attached to rachis, ovoid-ellipsoid, 0.8–1.1 × 0.3–0.6 mm, verrucose, beaked, beak slightly curved.

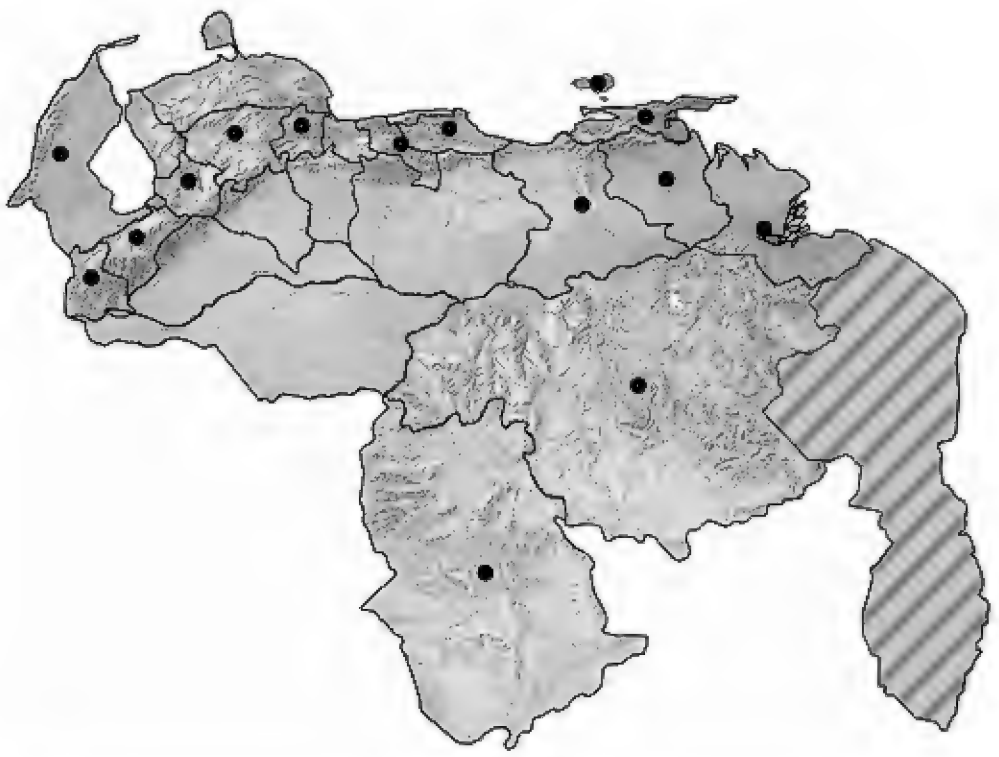
Restricted to South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, known from the Andes (Barinas, Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), and the Cordillera de la Costa (Anzoátegui, Aragua, Distrito Capital, Falcón, Miranda, Monagas, Sucre, and Yaracuy; Map 60). In the park, found on both slopes of Guaramacal; 1,600–2,350 m.

Callejas (2008) reported this species as occurring in the Venezuelan Guayana (Bolívar state) even though it was not included in the earlier published flora of that area (Steyermark and Callejas-Posada, 2003). Not having seen a voucher for this record, we are not including Bolívar in our distributional statement or map.

***Peperomia petrophila*** C. DC., Linnaea 37: 369. 1872; Steyermark, Fl. Venez. 2(2): 194–195. 1984.

*Peperomia petrophila* var. *brevipetiolata* Trel. & Yunck., Piperac. N. South Amer. 2: 457, fig. 402. 1950; Steyermark, Fl. Venez. 2(2): 195. 1984; Ortega et al., BioLlania 5: 51. 1987; Bono, Fl. Veg. Táchira 734. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 123. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 374. 2010.

Terrestrial herbs; stems erect, 5–18 cm long, erect, glabrous; shade-loving. Leaves alternate, clustered in the distal portion of the stem; leaf blades elliptic-lanceolate, 3.5–8(–9) × 1–2.5 cm, base acuminate-attenuate, margin minutely ciliate distally, apex



**MAP 59.** Distribution of *Peperomia obtusifolia* var. *obtusifolia*.

**MAP 60.** Distribution of *Peperomia peltoidea*.

acuminate, almost always ciliate, dark green above, silvery-green below, 5–7-plinerved, leathery-membranous; petioles 1–4 cm long, green, not surrounding the stem basally, pubescent or glabrous. Inflorescences simple, terminal or from the axes of upper leaves, solitary; peduncles filiform, 2.5–4.5 cm long, glabrous; spike erect, generally solitary, occasionally clustered in the distal portion of the stem, 4.7–9 cm long. Floral bracts orbicular- to subtriangular-peltate, membranous and translucent marginally. Fruit laterally attached to the rachis, globose-ovoid, 0.4–0.7 mm long, papillate and with prominent glands on the upper third of its surface, smooth basally.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, and Ecuador). In Venezuela, occurs in the Andes (Táchira and Trujillo) and in the Cordillera de la Costa (Distrito Capital and Miranda; Map 61). In the park, known from cloud forest on the south slope of Guaramacal; 1,600 m.

***Peperomia pilicaulis*** C. DC., Annuaire Conserv. Jard. Bot. Genève 21: 264. 1920.

*Peperomia ouabianae* C. DC., Candollea 1: 400. 1923; Steyermark, Fl. Venez. 2(2): 170–173, fig. 24, A3, B3. 1984 (excluding *Liesner et al. 12847*); Bono, Fl. Veg. Táchira 733. 1996.

Epiphytic herbs; climbing via roots at the nodes; stems ciliate-pubescent, hairs 2–4 mm long, translucent. Leaves alternate, rarely some apical leaves appearing opposite; leaf blades ovate-elliptic and orbicular on the same branch, 0.3–0.8(–1.2) × 0.4–1.2(–1.4) cm, base acute to obtuse, apex rounded or obtuse to subacute, dark green above, pale- or silvery-green below, obscurely palmately 3-nerved; petioles 0.2–0.4 cm long, pubescent. Inflorescences simple, terminal; peduncles filiform, 2.5–5 mm long, glabrous; spikes generally solitary, 1.5–6 cm long, erect, almost always pilose, sometimes glabrous. Floral bracts suborbicular-peltate; flowers loosely clustered on the rachis, sessile. Fruit sub-basally attached to the rachis, globose-ovoid, 0.4–0.6 mm long, smooth.

Central America and South America (Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, and Brazil). In Venezuela, found in the Andes (Portuguesa, Táchira, and Trujillo), the Cordillera de la Costa (Sucre and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 62). In the park, collected near the Divisioria de la Concepción and at an unspecified locality on "Cerro Guaramacal"; 1,700 m.

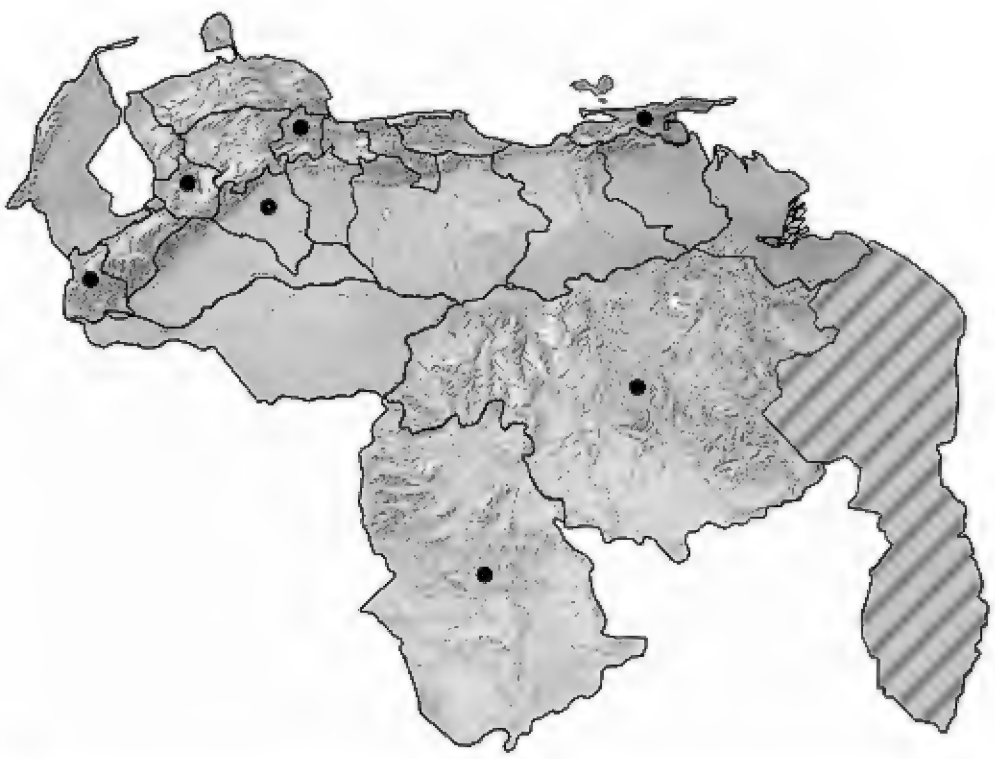
Although we consider *Peperomia ouabianae* to be a synonym of *P. pilicaulis* (see also Callejas, 1999, 2008), this is not universally accepted. The former species also is recognized as distinct (Bono, 1996; Steyermark and Callejas-Posada, 2003; Görts-van Rijn, 2007; Mathieu, 2007, 2024; Bernal, 2016). The type of *P. ouabianae* was collected on Mount Roraima and Trelease and Yuncker (1950) restricted the species to that mountain and neighboring Guyana. Steyermark and Callejas-Posada (2003) extended its range to the Cordillera de la Costa but not to the Andes.

At least one collection (*Liesner et al. 12847*) from Guaramacal cited by Steyermark (1984) as a voucher for *Peperomia ouabianae* var. *ouabianae* appears to be misidentified. It is referred here to *P. trinervula* C. DC.

***Peperomia portuguesensis*** Steyerm., Fl. Venez. 2(2): 195, fig. 26, A3. 1984.

Epiphytic herbs; stems glabrous or sparsely puberulent; rooting at basal nodes; branches widely-branching and reaching 5–25 cm tall. Leaves opposite or more frequently nodes 3-verticillate; leaf blades lanceolate-elliptic, 3–5.5 × 1–1.5 cm, base acute, apex attenuate to obtusely acuminate, glabrous, black-dotted below, palmately 3-nerved, veins inconspicuous above, slightly prominent below; petioles 1.5–5 cm long, papillate

**MAP 61.** Distribution of *Peperomia petrophila*.



**MAP 62.** Distribution of *Peperomia pilicaulis*.

puberulent, not sheathing. Inflorescences terminal, solitary spikes, 3–7 cm long, erect, pale green; peduncles 2–4 cm long. Floral bracts oval-oblong, peltate, 0.5–0.7 mm long. Fruit not seen.

Endemic to Venezuela where it is restricted to the lower slopes of the Andes (Portuguesa and Trujillo; Map 63). Our records are from the south slope of Guaramacal near the village of Guaramacal; 1,500–1,600 m.

***Peperomia quadrifolia*** (L.) Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 1: 57. 1815 [1816]; ibid. [qu.] 1: 69. 1815 [1816]; Steyermark, Fl. Venez. 2(2): 207–208, fig. 28, A1, B1, C1. 1984. *Piper quadrifolium* L., Sp. Pl., ed. 2, 1: 43. 1762.

Epiphytic herbs; stems erect, 6–15 cm long, > 0.4 mm thick; scandent; sun-loving. Leaves 4-verticillate; leaf blades obovate to spathulate, unequal in size, 0.4–1.2 × 0.3–0.6 cm, base cuneate, apex obtuse and emarginate or twice cleft, puberulent apically, pellucid-punctate, dull dark green above, dull green below, 2–3-palmately nerved, veins impressed above and below; petioles 0.1–0.6 cm long, glabrous. Inflorescences simple, axillary or terminal, solitary spikes, 0.8–2(–5) cm long, > 0.5 mm thick, erect, pale green or white; peduncles filiform, 0.4–1.7 cm long, glabrous. Floral bracts orbicular peltate; flowers loosely aggregated or widely separated one from the other on the rachis, sessile. Fruit laterally attached to the rachis, globose, asymmetric, 0.2–0.4(–10) mm long.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil). In Venezuela, found in the Andes (Mérida, Táchira, and Trujillo), the Sierra de Perijá (Zulia), and the Cordillera de la Costa (Aragua and Miranda; Map 64). In the park, known from cloud forest on the north slope of Guaramacal; 1,850 m.

This is the only species of *Peperomia* in Guaramacal with consistently emarginate leaf apices.

**MAP 63.** Distribution of *Peperomia portuguesensis.*

**MAP 64.** Distribution of *Peperomia quadrifolia.*

***Peperomia rhexiifolia*** Moritz ex C. DC., in de Candolle, Prodr. 16(1): 460. 1869 ("*rhexiæfolia*"); Steyermark, Fl. Venez. 2(2): 209–211, fig. 28, A4, B4. 1984 ("*rhexiaefolia*").

Epiphytic or saxicolous herbs; stems 20–50 cm long, erect, rooting at the basal nodes, glabrous. Leaves 3(4)-verticillate, occasionally opposite, often variable in shape and size on the same plant; leaf blades elliptic-lanceolate, elliptic-ovate to obovate, or oblong, 2.5–8.5(–10) × 1.4–3.5(–4.5) cm, base acute to subacute, slightly decurrent, apex acuminate, 3–7-palmatinerved, veins impressed to sulcate above, elevated and prominent below, pale green above, sometimes pink to reddish below, subcoriaceous; petioles sheathing basally, surrounding the stem, terete portion 0.5–1.3 cm long. Inflorescences simple, axillary or terminal; peduncles 0.4–2(–4.5) cm long; spikes 3–4 in the apex, 1.4–3(–10) cm long, erect, white to pale green, arched in fruit. Floral bracts orbicular-peltate, chartaceous; flowers densely clustered at anthesis, somewhat scattered in fruit. Fruit basally immersed and attached to the rachis, globose to ovoid, 0.6–0.8 mm long.

Found in Mexico, Central America, and South America (Colombia, Venezuela, Ecuador, and Bolivia). In Venezuela, found in the Andes (Mérida, Táchira, and Trujillo), the Sierra de Perijá (Zulia), and the Cordillera de la Costa (Anzoátegui, Aragua, Distrito Capital, Miranda, and Sucre; Map 65). Our sole voucher was found on the south slope of Guaramacal near El Santuario; 1,850–1,950 m.

Trelease and Yuncker (1950) listed this species as a synonym of *Peperomia angustata* Kunth but with doubt. *Peperomia angustata* is a more robust plant than *P. rhexiifolia*: it can reach up to 1 m in height and always has a single axillary spike (see Callejas, 2014).

***Peperomia rhombea*** Ruiz & Pav., Fl. Peruv. 1: 31, t. 46, fig. b. 1798; Steyermark, Fl. Venez. 2(2): 211–212, fig. 29, A2, B2. 1984.

**MAP 65.** Distribution of *Peperomia rhexifolia.*

**MAP 66.** Distribution of *Peperomia rhombea.*

*Peperomia* sp. A; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 376. 2010 ("*Peperomia* sp." as to Guaramacal material only).

Epiphytic herbs; scandent or erect; stems 15–20 cm long, 0.4–2 mm thick, puberulent or glabrescent. Leaves (3)4(5)-verticillate, occasionally opposite, uniform in shape and size throughout the plant; leaf blades elliptic-ovate, rhomboid to elliptic-lanceolate, 1.5–3.5(–4) × 0.5–1.7 cm, base cuneate, margin ± sinuate, apex obtuse to slightly acuminate, puberulent apically and along the margin, 3-palmatinerved, dark green and glabrous above, pale green and sparingly puberulent below; petioles 0.5–1.5 cm long, puberulent. Inflorescences terminal, simple; peduncles 2.5–4.5 cm long; spikes solitary, 2.2–6 cm long, erect, pale green or white. Floral bracts suborbicular, chartaceous, black-dotted, glabrous; flowers loosely clustered on the rachis, sessile. Fruit attached laterally to the rachis, obovoid or globose, 0.5–0.6 mm in diameter, papillate and granular.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil); expected to occur in Guyana. In Venezuela, known from the Andes (Mérida, Táchira, and Trujillo), the Sierra de Perijá (Zulia), and the Cordillera de la Costa (Aragua, Carabobo, Distrito Capital, Miranda, Monagas, Sucre, and Yaracuy; Map 66). Found in cloud forest on the north slope of the park; 1,800–2,300 m.

***Peperomia rotundata*** Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 1: 55, t. 12. 1815 [1816]; ibid. [qu.] 1: 67, t. 12. 1815 [1816]; Steyermark, Fl. Venez. 2(2): 212–216. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 696. 2003.

Only the nominate variety is found in Guaramacal.

***Peperomia rotundata*** var. ***rotundata***

Epiphytic, saxicolous, or terrestrial herbs; stems erect or ascending, green or sometimes reddish, sparingly pubescent with appressed hairs or puberulent; succulent. Leaves opposite or alternate on the same plant; leaf blades orbicular-ovate or ovate, 1.2–3.5(–5) × 0.5–3.5 cm, 3–5-nerved, base obtuse to acute, apex shortly attenuate or acute, densely or sparingly pubescent to glabrous above and below, 3–5-palmatinerved; petioles 4–18 mm long, minutely pubescent or glabrous, canaliculate or sheathing without surrounding the stem. Inflorescences simple, terminal or axillary, with 1(2–3) spikes per node; peduncles 3–15 mm long, sometimes widened, canaliculate. Floral bracts orbicular-peltate. Fruit basally attached to the rachis, globose, 0.8–1 mm long, verrucose.

Found in Central America, and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, found in the Andes (Mérida, Portuguesa, Táchira, and Trujillo) and in the Venezuelan Guayana (Amazonas; Map 67). Rare in the park, confined to cloud forest on the north slope of Guaramacal; 2,700–2,900 m.

The collection (*Dorr et al. 5004*) that we originally cited (Dorr et al., 2000) as the voucher for the presence of this species in the park is here referred to *Peperomia trinervula*. Nonetheless, a collection (*Stergios et al. 20743*) made after the publication of the catalog of the Guaramacal flora (Dorr et al., 2000) appears to represent the nominate variety of *P. rotundata*.

***Peperomia san-joseana*** C. DC., Linnaea 37: 372. 1872 ("*San-Joseana*").

*Peperomia pennellii* Trel. & Yunck., Piperac. N. South Amer. 2: 608, fig. 533. 1950; Steyermark, Fl. Venez. 2(2): 186–189, fig. 25, A3, B3, [C3]. 1984; Ortega et al., BioLlania 5: 51. 1983; Bono, Fl. Veg. Táchira 734. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 123. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 373. 2010.

**MAP 67.** Distribution of *Peperomia rotundata* var. *rotundata*.

**MAP 68.** Distribution of *Peperomia san-joseana*.

*Peperomia angularis* auct., non C. DC.; Steyermark, Fl. Venez. 2(2): 42, 43. 1984 (as to var. *angularis*).

Terrestrial herbs or epiphytes; stems erect, to 25 cm tall, angular in cross-section, 2–4 mm thick. Basal leaves alternate, apical ones opposite; leaf blades elliptic or elliptic-lanceolate, sometimes ovate, 2–7 × 1–4 cm, base obtuse to slightly rounded, apex obtuse to obtusely acute or obtusely acuminate, dark green above, pale green below, 3–5-palmatinerved, 3 innermost veins more prominent above; petioles 3–10 mm long. Inflorescences simple, terminal, with (1–)2–3 spikes; peduncles 5–25 mm long; spikes 1–12 cm long, 2–3 mm thick, erect, densely-flowered. Floral bracts suborbicular-peltate, 0.4–0.5 mm in diameter. Fruit sub-basally attached to rachis, subglobose or subglobose-ovoid, 0.8–1.2 mm long, slightly verrucose or not.

Found in Mexico, Central America, the West Indies (Hispaniola), and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, known from the Andes (Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Aragua, Distrito Capital, Falcón, Miranda, Monagas, and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 68). In cloud forest on the north slope of Guaramacal; 1,600 m.

According to Callejas (2014), it is possible that *Peperomia laevis* C. DC., described from Colonia Tovar, Aragua state, Venezuela, is an older name for *P. san-joseana*. Mathieu (2024), however, considered *P. laevis* to be a synonym of *P. alata*.

***Peperomia succulenta*** C. DC., J. Bot. 4: 142. 1866; Steyermark, Fl. Venez. 2(2): 235–237, fig. 30, A4, B4. 1984.

*Peperomia castanoensis* Trel. & Yunck., Piperac. N. South Amer. 2: 675. 1950.

*Peperomia gracilipeduncula* Yunck., Mem. New York Bot. Gard. 9(3): 324. 1957.

Terrestrial or epiphytic herbs; stems erect, 5–15(–20) cm long, rooting at basal nodes, glabrous. Leaves alternate, variable in shape and size along the same branch; basal blades typically obovate and spathulate, 1.5–3 × 1–1.8 cm, base attenuate to cuneate, apex obtuse and emarginate, apical blades obovate-lanceolate or oblanceolate, 3.5–8 ×1.2–2.5 cm, base attenuate to cuneate, apex acuminate, 3–7-plinerved, membranous to subcoriaceous; petioles 0.5–1 cm long, decurrent apically, clasping the stem basally. Inflorescences simple, terminal, spikes 4–10 cm long, erect, pale- to creamy-green; peduncles 0.8–1.6 cm long, glabrous. Floral bracts suborbicular-peltate, membranous, glandular-punctate; flowers densely clustered at anthesis, loosely clustered in fruit. Fruit basally or sub-basally attached to the rachis, globose, 0.3–4 mm in diameter, shortly apiculate, the apiculum oblique and triangular.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, reported from the Andes (Lara, Portuguesa, and Trujillo) and the Cordillera de la Costa (Aragua, Distrito Capital, Monagas, and Yaracuy; Map 69). In the park, collected on the south slope near La Divisoria de la Concepción; 1,500–1,600 m.

*Peperomia succulenta* is a densely caespitose herb with leaves that are variable in shape and size, and that dry thin and translucent (Mathieu and Callejas Posada, 2006). Trelease and Yuncker (1950) considered *P. succulenta* to be a synonym of *P. fragrans* C. DC., but the two species are distinct (see also Steyermark, 1984; Mathieu and Callejas Posada, 2006; Callejas, 2008). The latter species has conspicuous orange-brown glandular dots on both surfaces of the leaf blades, shorter and conspicuously decurrent petioles, and more narrowly attenuate-acuminate leaf apices than *P. succulenta*. *Peperomia fragrans* appears to be restricted to the Cordillera de la Costa although Steyermark (1984) cited a doubtful record (*Trujillo 6894*) from Lara state.

MAP 69. Distribution of *Peperomia succulenta*.

MAP 70. Distribution of *Peperomia talinifolia*.

***Peperomia talinifolia*** Kunth, in H. B. K. [fol.] 1: 51, t. 8. 1815 [1816]; ibid. [qu.] 1: 62, t. 8. 1815 [1816].

*Peperomia umbellifera* Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 2: 856, fig. 509. 1950; Steyermark, Fl. Venez. 2(2): 265–266, fig. 35, A4. 1984; Ortega et al., BioLlania 5: 52. 1987; Bono, Fl. Veg. Táchira 737. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 375–376. 2010.

Terrestrial herbs; stems 50–150 cm tall, 4–6 mm thick, decumbent basally, glabrous; succulent. Leaves alternate or very close to one another and appearing verticillate, sometimes opposite in apical branches; leaf blades elliptic-ovate, 7–15 × 2.5–5 cm, base cuneate to decurrent, apex rounded or broadly acute to subacuminate, dark green above, pale green or silvery-green below, 2–5-pinnatinerved, coriaceous; petioles winged, 0.5–2.5(–4) cm long, glabrous. Inflorescences terminal or axillary, ending in 2–5 axes, each 5–16 cm long, spikes 3–7 in umbellate groups, 2–13 cm long, yellowish, sparingly flowered, rachis glabrous; peduncles reddish, 0.4–4.5 cm long, 1-bracteate. Floral bracts orbicular-peltate, 0.2–0.3 mm long. Fruit sub-basally attached to rachis, globose-ovoid, 1 × 0.4–0.6 mm, shortly beaked.

Found in Central America, the West Indies (Greater Antilles), and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia). In Venezuela, restricted to the Andes (Mérida, Táchira, and Trujillo; Map 70). In the park, collected in Qda. Jirajara on the south slope of Guaramacal near the summit of the Boconó–Guaramacal road; 2,500–3,150 m.

According to Mathieu (2024), *Peperomia talinifolia* and *P. umbellifera* differ in the venation of their leaves. We do not see significant differences in venation in images of their type specimens and adopt the synonymy proposed by Callejas (1999).

***Peperomia tenella*** (Sw.) A. Dietr., Sp. Pl., ed. 6, 1: 153. 1831; Steyermark, Fl. Venez. 2(2): 244–245. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 697. 2003. *Piper tenellum* Sw., Prodr. 16. 1788.

*Piper tenella* var. *glabra* C. DC., in de Candolle, Prodr. 16(1): 397. 1869.

Only the nominate variety is found in Venezuela.

***Peperomia tenella*** var. ***tenella***

Steyermark, Fl. Venez. 2(2): 245–246, fig. 33, A1, B1. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 698. 2003.

Terrestrial, saxicolous, or epiphytic herbs; flowering shoots erect; stems 5–12 cm tall; caespitose. Leaves alternate, distichous; basal leaves smallest, upper leaves uniform in size and shape; leaf blades generally elliptic, some ovate or obovate, 0.4–1.2(–2) × 0.2–0.6(–1) cm, base obtuse to subacute, apex inconspicuously to clearly emarginate, obtuse, usually glabrous above and below or with cilia dispersed along the margin, palmately 3-nerved; petioles 0.1–0.3 cm long. Inflorescences simple, terminal, spikes 1.5–8 cm long, pale green; peduncles 4–15 mm long. Flowers scattered along the rachis; floral bracts suborbicular-peltate. Fruit basally attached to the rachis, pedicellate, pedicel 1–1.4 mm long, fruit body ellipsoid, 1–1.4 mm long, rugose.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, possibly Guyana, Peru, and Brazil). In Venezuela, found in the Andes (Lara, Mérida, Táchira, and Trujillo), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Cojedes, Distrito Capital, Falcón, Guárico, Miranda, Monagas, and Sucre), and the Venezuelan Guayana (Amazonas and Bolívar; Map 71). In the park, found in cloud forest on the south slope of Guaramacal and near the village of Guaramacal; 1,500–1,900 m.

MAP 71. Distribution of *Peperomia tenella* var. *tenella*.

MAP 72. Distribution of *Peperomia tequendamana*.

*Peperomia tenella* is easily recognized because of its small size, single stems with alternating simple leaves, and terminal spikes with pedicellate fruit.

*Peperomia tenella* var. *tyleri* (Trel.) Steyerm., also recognized by Steyermark (1984) as occurring in Venezuela, is considered a synonym of *P. tenuipes* Trel. (Mathieu and Callejas Posada, 2006; Callejas, 2014; Mathieu, 2024).

***Peperomia tequendamana*** Trel., J. Wash. Acad. Sci. 16: 207. 1926. *Peperomia rotundata* var. *tequendamana* (Trel.) Steyerm., Fl. Venez. 2(2): 217. 1984; Bono, Fl. Veg. Táchira 735. 1996; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 374. 2010.

FIGURE 5E

Epiphytic or terrestrial herbs; hanging (when epiphytic) or decumbent; stems 10–35 cm long, reddish, densely rusty pubescent, hairs 1–4 mm long, rigid. Leaves alternate, uniform in size and shape; leaf blades broadly elliptic or ovate-elliptic, 0.6–2.8 × 1–2.5 cm, base rounded, apex obtuse or rounded, dark green above, pale green with red or pink spots below, densely pubescent above and below, 3–5-veined, succulent; petioles reddish, 0.4–1.2 cm long, canaliculate, densely villous. Inflorescences mostly solitary, sometimes simple, terminal or axillary, spikes 2–6.5 cm long, pendent, reddish when mature, rachis glabrous; peduncles 1–2.8 cm long, ebracteate. Floral bracts ovoid or subovoid, yellowish white. Fruit globose to ovoid, apically beaked.

Found in Central America (Costa Rica and Panama) and northern South America (Colombia, Venezuela, and Ecuador, including the Galapagos Islands). In Venezuela, known from the Andes (Barinas, Mérida, Táchira, and Trujillo) and the Sierra de Perijá (Zulia; Map 72). In the park, found in páramo and subpáramo near the summit of Guaramacal and near the Laguna del Pumar; 2,900–3,100 m.

We follow Mathieu and Callejas Posada (2006) in recognizing this taxon as a species rather than a variety because its alternate leaves and long golden hairs are quite distinct from the opposite leaves and white, shorter and suberect hairs that characterize *Peperomia rotundata*.

***Peperomia tetraphylla*** Hook. & Arn., Bot. Beechey Voy. 97. 1841 [1832]; Steyermark, Fl. Venez. 2(2): 251–255, fig. 32, A4, B4, C4, D4, E4. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 698. 2003.

Only the nominate variety is found in Venezuela.

***Peperomia tetraphylla*** var. ***tetraphylla***

FIGURE 5F

Epiphytic herbs; erect, occasionally creeping; stems 6–10 cm long, loosely to densely branched, pellucid-punctate, puberulent, hairs retrorse; succulent. Leaves verticillate, generally 4 per node, uniform in shape and size; leaf blades elliptic to ovate, 0.5–1.5(–2) × 0.6–1 cm, base cuneate, apex obtuse or slightly acuminate, glabrous above, sparingly to densely puberulent below and pellucid-punctate or papillate, 2-palmatinerved; petioles 1–1.5 mm long, densely puberulent. Inflorescences simple, terminal, spikes solitary, erect, pale green or yellow, rachis 1.5–3.8(–4) cm long, densely and shortly pilose, partially concealed by the floral bracts; peduncles 1–2.5(–4) cm long, densely and shortly pilose. Floral bracts orbicular-peltate; flowers densely clustered on the rachis, sessile. Fruit basally attached to or immersed in the rachis, subcylindrical, 0.5–1 mm long, pellucid-punctate, umbonate-mammiform.

A widespread species that occurs in Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay), Africa, Madagascar, the Arabian Peninsula (Yemen), Asia, Australia, and the Pacific Islands. In Venezuela, found in the Andes (Lara, Mérida,

Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Aragua, Distrito Capital, Falcón, Guárico, Miranda, Sucre, and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 73). In the park, found in forest on both slopes of Guaramacal; (1,550–)1,850–2,550 m.

*Peperomia tetraphylla* was considered a synonym of *P. reflexa* (L. f.) A. Dietr. by Trelease and Yuncker (1950), but the latter name is a later homonym of *P. reflexa* Kunth.

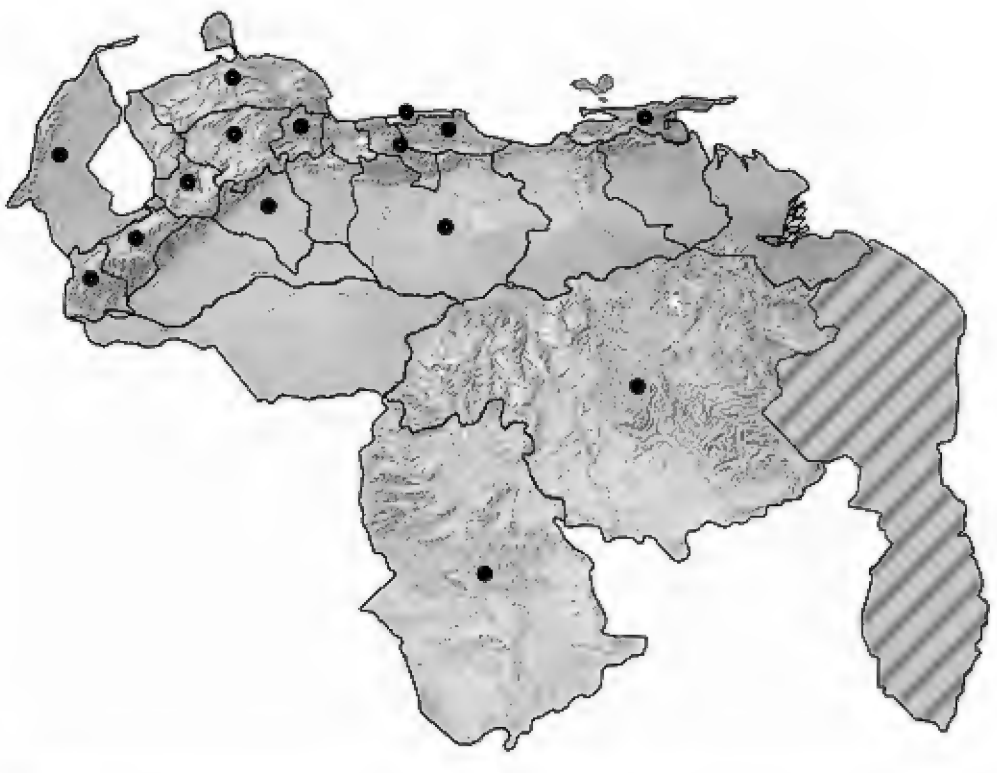
***Peperomia tovariana*** C. DC., in de Candolle, Prodr. 16(1): 404. 1869; Steyermark, Fl. Venez. 2(2): 258–260, fig. 34, A2, B2, C2. 1984.

*Peperomia tovariana* var. *subcaespitosa* Trel. & Yunck., Piper. N. South Amer. 2: 709, fig. 632. 1950.

*Peperomia araguana* Trel. ex V. M. Badillo, in Pittier et al., Cat. Fl. Venez. 1: 244. 1945, nom. nud.

Epiphytic or saxicolous herbs, 5–15 cm tall, erect, rooting at basal nodes; stems ciliate pubescent, hairs 0.3–0.5 mm long. Leaves alternate, distichous, variable in shape and size within the same branch; leaf blades ovate, orbicular, sometimes reniform, 0.4–0.7 × 0.2–0.6 cm, base rounded or obtuse, margin ciliate, apex obtuse or acuminate, pilose above, glabrous below, imperceptibly 3-nerved, leathery-membranous; petioles 0.2–0.5 mm long, glabrous or sparsely pilose. Inflorescences simple, terminal, spikes 1–4 cm long, yellowish green; peduncles 0.4–1 mm long, filiform. Fruits ovoid, asymmetric, pedicellate; pedicels 0.5–1 mm long, surface smooth.

Found in Mexico, Central America, and South America (Colombia, Venezuela, Ecuador, Peru, and Bolivia); introduced in the West Indies (Hispaniola and Jamaica). In Venezuela, known from the Andes (Lara, Mérida, Táchira, and Trujillo) and the Cordillera de la Costa (Aragua, Falcón, Sucre, and Yaracuy; Map 74). In the park, collected in cloud forest; 1,900–2,300 m.



**MAP 73.** Distribution of *Peperomia tetraphylla* var. *tetraphylla*.

**MAP 74.** Distribution of *Peperomia tovariana*.

***Peperomia trichopus*** Trel., in Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2): 101. 1936; Steyermark, Fl. Venez. 2(2): 260–261, fig. 35, A3, B3. 1984.

Epiphytic herbs; creeping; stems elongate, 0.2–0.4 mm thick, reddish, rooting at the nodes, glabrous; almost always growing in dense colonies. Leaves 3–8-verticillate; leaf blades obovate to elliptic-obovate, 0.3–0.7 × 0.2–0.4 cm, base acute to subcuneate, apex rounded, sparingly appressed pubescent above, glabrous below, 3-palmatinerved, leathery-subcoriaceous; petioles 1.5–4 mm long, glabrous. Inflorescences simple, terminal or rarely axillary, solitary spikes, 1.2–3.5 cm long, 0.2–0.4 mm thick; peduncles filiform, 2–4 cm long (longer than the spikes), glabrous. Floral bracts suborbicular-peltate, 0.6–0.7 mm long, with pale glands. Fruit ellipsoid, 0.8–1 mm long, stipitate, apex obliquely spherical.

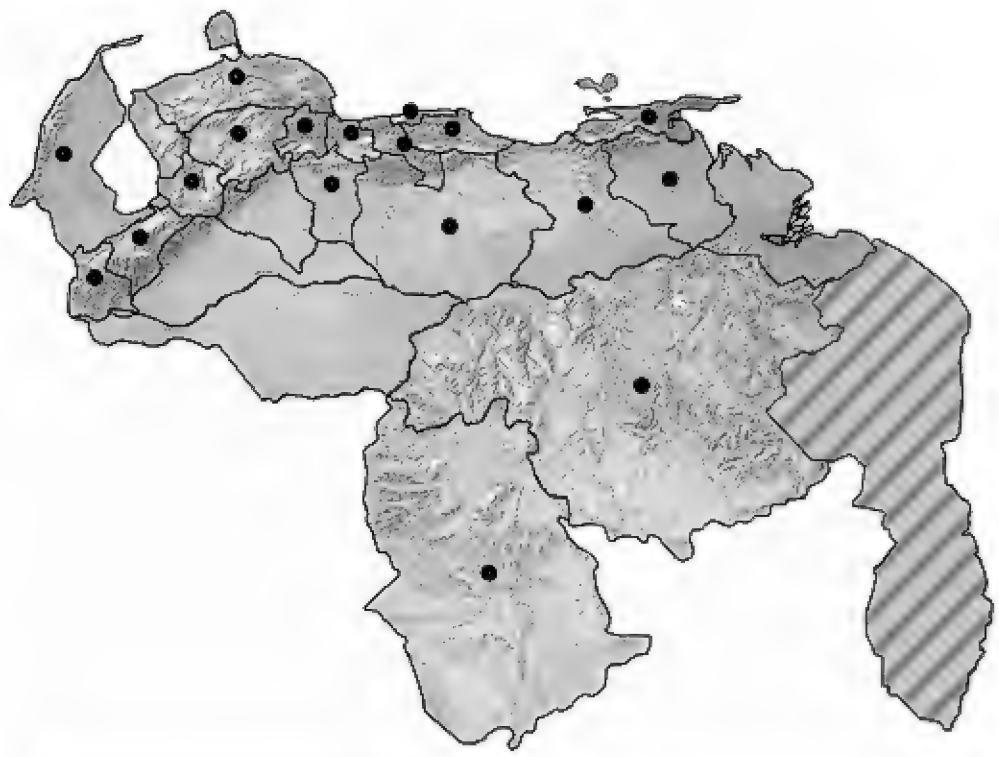
Found in South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, known from the Andes (Lara, Mérida, Portuguesa, and Trujillo) and the Cordillera de la Costa (Carabobo and Monagas; Map 75). Our sole record is from the south slope of Guaramacal between El Campamento and El Mogote; 1,800 m.

***Peperomia trinervula*** C. DC., in de Candolle, Prodr. 16(1): 420. 1869. *Peperomia rotundata* var. *trinervula* (C. DC.) Steyerm., Fl. Venez. 2(2): 217–219, fig. 29, A4, B4. 1984; Ortega et al., BioLlania 5: 52. 1987; Bono, Fl. Veg. Táchira 735. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001]; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 696–697. 2003; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 374–375. 2010.

FIGURE 5G,H

*Peperomia ouabianae* var. *ouabianae* auct., non C. DC.; Ortega et al., BioLlania 5: 51. 1987; Dorr et al., Contr. U.S. Natl. Herb. 40: 123. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 373. 2010.

MAP 75. Distribution of *Peperomia trichopus*.



MAP 76. Distribution of *Peperomia trinervula*.

*Peperomia rotundata* var. *rotundata* auct., non Kunth; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001] (as to *Dorr et al. 5004*); Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 374. 2010 (as to *Dorr et al. 5004*).

Epiphytic, saxicolous, or terrestrial herbs; stems erect, ascending, 15–60 cm tall, green or sometimes bright reddish (when fresh), appressed pubescent, hairs 0.2–0.4 mm long, rooting at basal nodes; succulent. Leaves alternate or appearing opposite in terminal buds; leaf blades orbicular to ovate, rarely elliptical, 1.5–3.5(–4.5) × 0.5–3 cm, base shortly acute, apex shortly attenuate or acute, 3–5-nerved; petioles 0.4–2.4 cm long, pubescent, canaliculate or sheathing without surrounding the stem. Inflorescences simple, sometimes compound, terminal or axillary, spikes almost always solitary, sometimes 2–4-umbellate, 2–6 cm long, erect; peduncles 3–15 mm long, sometimes widened, canaliculate. Floral bracts orbicular-peltate. Fruit basally attached to the rachis, globose, 0.8–1 mm long, verrucose.

Found in Central America and South America (Colombia, Venezuela, possibly Guyana, Ecuador, Peru, Bolivia, and Brazil). Widespread in Venezuela, known from the Andes (Lara, Mérida, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Anzoátegui, Aragua, Carabobo, Cojedes, Distrito Capital, Falcón, Guárico, Miranda, Monagas, Sucre, and Yaracuy), and the Venezuelan Guayana (Amazonas and Bolívar; Map 76). In the park, very common in cloud forest on both slopes of Guaramacal and on the Fila de Agua Fría; 1,600–3,100 m.

Although Steyermark (1984) reduced *Peperomia trinervula* to a variety of *P. rotundata*, Mathieu (2024) believed it preferable to maintain this taxon at specific rank. *Peperomia trinervula* has alternate leaves that are only opposite at some of the branching nodes, whereas *P. rotundata* has opposite leaves at every single node, a different leaf shape, and different hair types.

***Peperomia* sp. B**

Epiphytic herbs; erect, stems 15–20 cm tall, 2–3 mm thick (when dry), angular in cross-section, glabrous or minutely tomentose-pubescent; rooting from basal nodes. Leaves opposite, almost always 3(4)-verticillate in the apices of branches, heterophyllous with minute leaves irregularly arising from lower stems, solitary or in the axils of other leaves; leaf blades (non-reduced) elliptic to obovate, 2–3.5 × 0.6–1.8 cm, base acute or cuneate, margin smooth, ciliate, apex rounded to obtuse, leaf-blades (reduced) ovate or orbicular, ~2–5 mm in diameter, all leaf blades densely glandular-punctate above and below; petioles (non-reduced leaves) 6–15 mm long, usually channelled (canaliculate) and sheathing at the base, tomentose-pubescent. Inflorescences terminal, 1–2 spikes in the apices of branches, 2–5 cm long, usually curved or even pendulous when mature; peduncles 0.5–1.4 cm long. Floral bracts orbicular, 1–1.2 mm in diameter. Fruit globose, 0.4–0.6 mm long, brown.

At present, known only from collections made in Guaramacal National Park in Venezuela (Trujillo; Map 77). Found in cloud forest on the north slope of Guaramacal; 1,850–1,900 m.

This taxon is distinctive in having angular stems, glandular-punctate leaves above and below, and in being heterophyllous with the non-reduced leaves verticillate and the reduced leaves solitary or in the axils of other leaves.

***Species excluded from the flora***

*Peperomia gehrigeri* Trel. & Yunck. is excluded from the flora of Guaramacal. It was attributed to the flora by Ortega et al. (1987), but their voucher (*Badillo 3547*, MY, VEN) was collected on the road between Trujillo and Boconó, which is not within nor near the boundaries of Guaramacal National Park.

MAP 77. Distribution of *Peperomia* sp. B.

## *Piper* L.

*Piper* L., Sp. Pl. 28. 1753.

*Ottonia* Spreng., Neue Entdeck. Pflanzenk. 1: 255. 1820.

*Macropiper* Miq., Comment. Phytogr. 32, 35. [16–21 Mar] 1840; ibid., Bull. Sci. Phys. Nat. Neerl. 1839: 447, 449. [Jan-Jun] 1840.

*Pothomorphe* Miq., Comment. Phytogr. 32, 36. [16–21 Mar] 1840, nom. superfl.; ibid., Bull. Sci. Phys. Nat. Neerl. 1839: 447, 450. [Jan-Jun] 1840.

*Trianaeopiper* Trel., Proc. Amer. Philos. Soc. 67: 50. 1928.

Small trees, shrubs, subshrubs, herbs, or lianas; dioecious, monoecious, or hermaphroditic; terrestrial or hemiepiphytic; stems loosely or profusely branched; many species with enlarged and prominent nodes. Prophylls solitary and lateral when present. Leaves alternate; leaf blades entire or lobed only at the base, sometimes peltate, sometimes succulent; petioles short or long, margins narrowly to conspicuously winged, sheathing only at the base or the entire length, persistent or caducous. Inflorescences terminal or axillary, simple spikes, compound racemes, or umbels of spikes. Flowers dispersed or densely aggregated within a spike; floral bracts variable in form and size, stipitate or sessile, the majority fimbriate; stamens 2–6; anthers longitudinally dehiscent, oblique or horizontal; ovary generally sessile, with or without a style; stigmas 2–5. Fruit generally free from the rachis of the spike, sessile or pedicellate.

A pantropical and subtropical genus of ~1,500–2,400 species found in Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and Uruguay), Africa, Madagascar, Asia, Australia, and the Pacific Islands; adventive in North America (USA). Approximately 146 species occur in Venezuela.

References. Trelease and Yuncker (1950); Tebbs (1989a, 1989b, 1990, 1993b); Jaramillo and Callejas (2004); Quijano-Abril et al. (2006); Jaramillo et al. (2008).

*Piper nigrum* L., native to India, is the most commercially important member of this genus. Its dried fruit are used as a spice and seasoning (i.e., black and white pepper). In fact, it may be the world's most widely traded spice. It has been cultivated inVenezuela, but not in the Andes nor in Guaramacal.

### KEY TO THE SPECIES OF *PIPER*

1a. Spikes 2–14, umbelliform on a common peduncle; leaf base deeply and widely cordate with rounded subequal lobes . . . . . ***P. umbellatum***

1b. Spikes solitary on a peduncle; leaf base variable, not deeply and widely cordate . . . . . 2

2a. Leaves peltate; petioles inserted 3–4 cm from margin of leaf base below . . . . . ***P. neovenezuelense***

2b. Leaves never peltate; petioles attached to margin of leaf base . . . . . 3

3a. Stems, leaves, and petioles glabrous (sometimes petioles and veins puberulent) . . . . . 4

4a. Leaf blades ovate to suborbicular-ovate or subelliptic, apex generally acute; mature inflorescences 3–40 cm long . . . 5

5a. Plants eglandular; petioles purple, wine-red, or pink, sheathing-winged, the sheath extending to 10 mm past the base of the leaf blade; inflorescences pendulous, 10–40 cm long . . . . . ***P. longispicum***

5b. Plants abundantly glandular throughout; petioles green, sheathing only to the middle, winged; inflorescences erect or ascending, 3–9 cm long . . . . . ***P. tristemon***

4b. Leaf blades elliptic, ovate, or lanceolate (or some variant of these shapes); mature inflorescences (1.5–)2–10 cm long . . . . . 6

6a. Lianas or hemiepiphytes; leaf base oblique, rounded, cordiform, or subauriculate; petioles 3–7 mm long; mature inflorescences red-purple or violet . . . . . ***P. morii***

6b. Shrubs or small trees; leaf base cuneate, acute, or rounded; petioles 3–25 mm long; inflorescences green, yellow, or white . . . . . 7

7a. Leaves 4–9 ×1.5–2.3 cm; leaf blades linear-lanceolate or lanceolate . . . . . ***P. calvarii***

7b. Leaves 5–25 × 2.5–10 cm; leaf blades elliptic, ovate, or lanceolate (or some variant of these shapes), sometimes narrowly-lanceolate . . . . . 8

8a. Branches, petioles, and leaf blades densely punctate-glandular; inflorescences erect in flower, pendulous in fruit, thickened when mature, to 10 mm thick . . . . . ***P. phytolaccifolium***

8b. Plants eglandular or only leaf blades glandular with glands scattered above and below; inflorescences erect in flower and fruit, not noticeably thickened when mature, 2–4 mm thick. . . . . 9
9a. Leaf base rounded or acute, slightly oblique or oblique, not truncate; leaf blades with 3–6 secondary veins on each side of the midrib, tertiary veins reticulate and inconspicuous. . . . . 10
10a. Leaf blades ovate, elliptic-ovate, or oblong-elliptic, 4–10 cm wide, apex acuminate . . . . . ***P. aequale***
10b. Leaf blades elliptic, ovate-lanceolate, or lanceolate-elliptic, 1.5–6 cm wide, apex long acuminate . . . . . 11
11a. Leaf apex slightly falcate; spikes green or greenish-white, rachis 3–6 cm long . . . . . ***P. sotobosquense***
11b. Leaf apex not falcate; spikes cream-colored, rachis 6–10 cm long . . . . . ***P. oblongum***
9b. Leaf base oblique to ± truncate, not rounded or acute; leaf blades with 6–10 secondary veins on each side of the midrib, tertiary veins slightly prominent below . . . . . ***P. pervenulosum***
3b. Stems, leaves, and/or petioles (or at least one of these) pubescent . . . . . 12
12a. Leaf blades pubescent, sometimes asperous or rough to the touch (when dry). . . . . 13
13a. Leaf blades widely-ovate to suborbicular, 8–14 cm wide, often widest below the middle of the blade, base oblique, rounded, truncate, or cordiform; spikes 6–10 mm thick . . . . . ***P. viridistachyum***
13b. Leaf blades lanceolate, elliptic, elliptic-lanceolate, or elliptic-ovate, 3–10.5 cm wide, sometimes widest below the middle of the blade, base oblique, never truncate or cordate; spikes < 5 mm thick. . . . . 14
14a. Venation of leaf surface below conspicuously alveolate . . . . . ***P. bredemeyeri***
14b. Venation of leaf surface below not alveolate . . . . . 15
15a. Inflorescences arching or recurved; stems villous-pubescent, hairs 1–3 mm long, white or cream . . . . . ***P. aduncum***
15b. Inflorescences erect; stems glabrescent or with hairs 0.2–0.5 mm long, light brown to ferruginous . . . . . ***P. hispidum***
12b. Leaf blades glabrous or pubescent only on the veins (or petioles), almost always smooth to the touch (when dry) . . . . . 16
16a. Leaf blades rugose to bullate or verrucose above, alveolate below, margin crenulate; peduncles 1–3.5 cm long . . . . . ***P. diffamatum***
16b. Leaf blades not rugose or verrucose above, not alveolate below, margin entire; peduncles 0.5–2 cm long . . . . . 17
17a. Spikes 5–11 cm long, 2–3 mm thick, white. . . . . ***P. dilatatum***
17b. Spikes 3–5 cm long, 3–6 mm thick, white or gray . . . . . ***P. prunifolium***

***Piper aduncum*** L., Sp. Pl. 29. 1753; Steyermark, Fl. Venez. 2(2): 303–307, fig. 38, A1, B1, C1, D1, E1, F1, G1, H1. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 714. 2003; Duno de Stefano and Aymard, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 622. 2007.

*Piper angustifolium* var. *cordulatum* C. DC., in Candolle, Prodr. 16(1): 286. 1869. *Piper aduncum* var. *cordulatum* (C. DC.) Yunck., Lilloa 27: 129. 1955; Steyermark, Fl. Venez. 2(2): 305, 307–309. 1984; Bono, Fl. Veg. Táchira 737. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001]; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 714. 2003; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 376. 2010.

Our material can be referred to the nominate variety.

### *Piper aduncum var. aduncum*

FIGURE 6A–C

Shrubs or small trees, 2–4(–8) m tall; stems branched, villous-pubescent, hairs 1–3 mm long, white or cream. Prophylls 5–30 mm long, dorsally glabrous or densely hirsute, caducous. Leaves ± distichous, regular in shape and size the length of axes; leaf blades elliptic-ovate to elliptic-lanceolate, asymmetrical, 10–20 × 3–7(–9) cm, base oblique, unequally rounded to obtuse, apex narrowly acuminate, densely rough scabrous above, densely soft villous below, pinnatinerved with 5–6 secondary veins each side of the midrib, green or greenish-yellow above, paler green below, membranous; petioles 3–10 mm long, ± pubescent, sheathing only at the base; stipules at the base of flowering nodes or extending to the middle of the petiole in sterile nodes, 2–4 mm long, caducous. Inflorescences arching or recurved, yellowish white at anthesis, green in fruit; peduncles 1–1.7 cm long, hirsute or strigose, eventually glabrescent; rachis 4–12(–14) cm long, glabrous. Floral bracts narrowly triangular, 0.3 mm wide, densely fimbriate. Fruit ovoid, rounded, or trigonous, 0.8–1 mm long, apically truncate and depressed, glabrous or papillate.

Widespread and found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina, and possibly Uruguay); adventive in North America (USA), Asia, and the Pacific Islands. Widespread in Venezuela where it is known from the Andes (Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia),

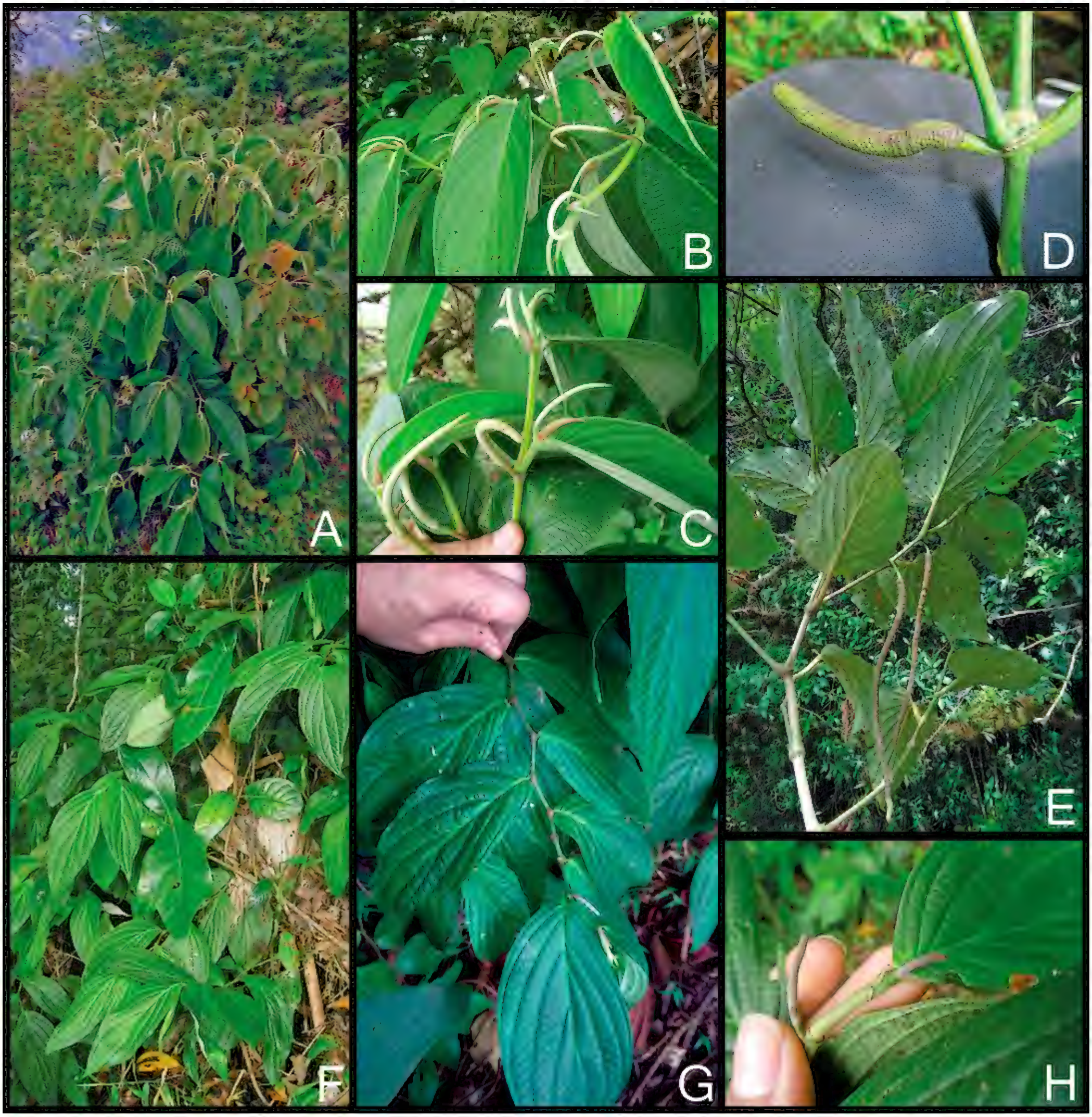



**FIGURE 6. A–C.** Piperaceae, *Piper aduncum* L. var. *aduncum*. A. Habit. B. Leaves and inflorescences. C. Prophylls. **D.** *P. aequale* Vahl. Infructescence and swollen node. **E.** *P. longispicum* var. *glabratum* (Yunck.) Steyerm. Leaf surface below and 2 pendulous inflorescences. **F–H.** *P. morii* (Steyerm.) Dorr & S. M. Niño. F. Habit. G. Branch with leaves (note inflorescences toward branch apex). H. Inflorescence and prophyll. (A–H, photographer D. Canelón).

the Cordillera de la Costa (Aragua, Distrito Capital, Falcón, Guárico, Miranda, Sucre, and Yaracuy), Dependencias Federales, the Venezuelan llanos (Anzoátegui, Barinas, and Cojedes), and the Venezuelan Guayana (Amazonas and Bolívar; Map 78). In the park, collected on the north slope of Guaramacal; 1,800–2,500(–3,000) m.

The extremely rough upper leaf surface and soft lower leaf surface combined with arching inflorescences make *Piper aduncum* easy to recognize among the species of *Piper* occurring in Guaramacal.

Although Steyermark (1984) recognized three varieties of *Piper aduncum*, the nominate variety and *P. aduncum* var. *cordulatum* are scarcely separable. Both are scabrous and said to differ only in minor pubescence characters. *Piper aduncum* var. *garcia-barrigae* Trel. & Yunck., however, is distinct in that its leaves are not scabrous.

***Piper aequale*** Vahl, Eclog. Amer. 1: 4, t. 3. 1796 [1797]; Steyermark, Fl. Venez. 2(2): 311–314, fig. 39 A2, B2, C2, D2. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 714–715. 2003; Duno de Stefano and Aymard, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 622. 2007.

FIGURE 6D

*Piper caripense* Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 1: 40. 1815 [1816]; ibid. [qu.] 1: 48. 1815 [1816].

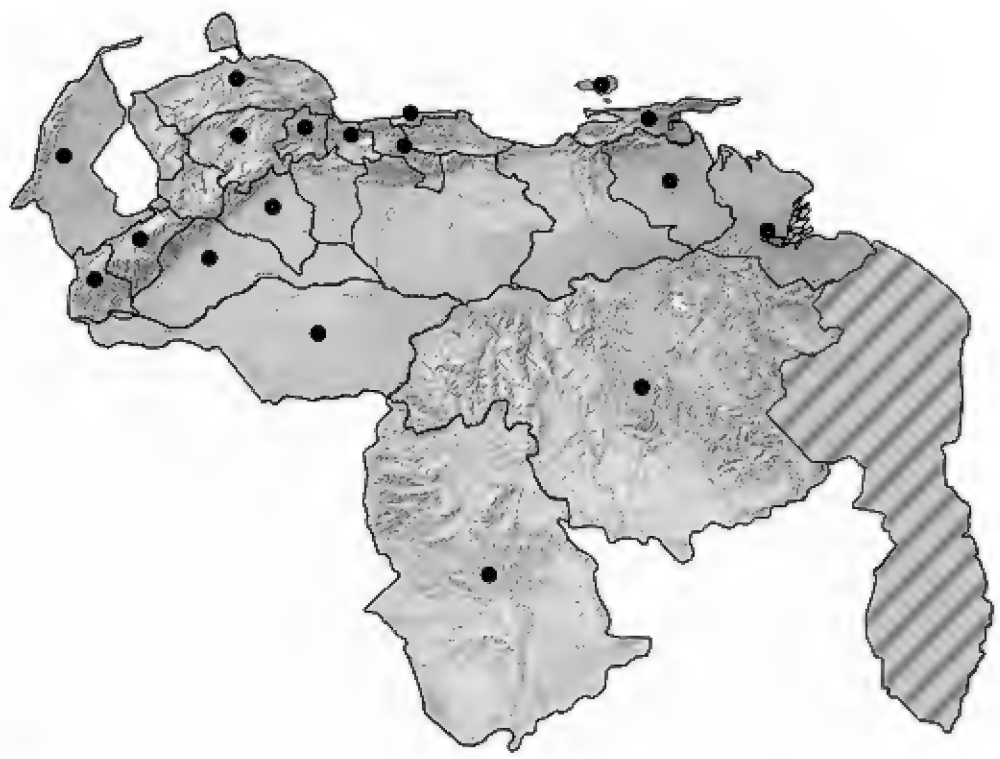
Shrubs 0.5–2(–6) m tall, branched; stems striate or channeled, glabrous. Prophylls 1–2 cm long, glabrous or papillate, caducous. Leaves generally distichous, uniform in shape and size the length of the axes; leaf blades ovate, elliptic-ovate, or oblong-elliptic, 7–15(–20) × 4–10 cm, base rounded or acute, very slightly oblique, slightly decurrent on the petiole, apex acuminate, glabrous above and below, pinnatinerved with 4–6 secondary veins each side of the midrib, veins generally ascending, diverging at an angle of 45–70° from the midrib, widely spaced and not equidistant, tertiary veins reticulate and inconspicuous, veins visible and scarcely raised above, midrib and secondary veins conspicuously raised below, firmly membranous; petioles 0.5–2 cm, glabrous; stipules at the base of nodes, 2–6 mm long, caducous. Inflorescences erect, white or cream at anthesis, grayish green in fruit; peduncles 6–12 mm long, glabrous; rachis 3.5–8.5 cm long, glabrous. Floral bracts triangular-oblong or subrhombic, 0.2 mm long, shortly fimbriate; flowers loosely to densely clustered on the rachis. Fruit obovoid or obpyramidal, 0.7–0.8 mm long, rounded or trigonous apically, glabrous or minutely papillate.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, and Brazil). Widespread in Venezuela, occurring in the Andes (Lara, Mérida, Portuguesa, and Táchira), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Aragua, Carabobo, Distrito Capital, Falcón, Monagas, Sucre, and Yaracuy), Nueva Esparta, the Venezuelan llanos (Apure and Barinas), and the Venezuelan Guayana (Amazonas, Bolívar, and Delta Amacuro; Map 79). In the park, found in cloud forest on both slopes of Guaramacal; 1,550–1,950 m.

Callejas (2014) concluded that *Piper aequale* s. str. is endemic to Montserrat, an island in the Lesser Antilles. If *P. aequale* is restricted to the West Indies, then the correct name for the species treated here is *P. caripense* Kunth, which was described from material collected near Caripe in present-day Monagas state.

According to Tebbs (1990), *Piper aequale* var. *glanduligerum* (C. DC.) Steyerm. (≡ *Piper glanduligerum* C. DC.) is a synonym of *P. schiedeanum* Steud. Steyermark (1984) considered *P. pervenulosum* Yunck. to be a synonym of *P. aequale* var. *glanduligerum*, but we accept *P. pervenulosum* as a distinct species (see below).

**MAP 78.** Distribution of *Piper aduncum* var. *aduncum*.



**MAP 79.** Distribution of *Piper aequale*.

***Piper bredemeyeri*** J. Jacq., Ecl. Pl. Rar. 1: 125, t. 84. 1811 [1816]; Steyermark, Fl. Venez. 2(2): 359–362, fig. 45, A3, B3, C3, D3, E3. 1984.

*Piper bredemeyeri* var. *angustifolium* Trel. & Yunck., Piperac. N. South Amer. 1: 186. 1950.

*Piper bredemeyeri* f. *escabridum* Steyerm., Fl. Venez. 2(2): 361. 1984.

Shrubs, 1–3 m tall; branched; stems canaliculate, pubescent, hirsute-hispid or pilose. Prophylls 1–2 cm long, marginally hirsutulous-villous, caducous. Leaves pendulous, uniform in shape and size the length of the axes; leaf blades asymmetric, lanceolate to elliptic-ovate, 7–20(–25) × 4.5–9.5 cm, base obtuse, rounded to subcordate, conspicuosly oblique (one side often 2–5 mm shorter than the other), apex long acuminate, almost always verrucose and scabrous above, conspicuously alveolate below and pilose-hispidulous, pinnatinerved with 4–5 veins each side of the midrib, ascending, coriaceous; petioles 5–18 mm long, hirsutulous, glabrescent; stipules prominent in sterile nodes, 1–2 mm long, caducous. Inflorescences curved distally at anthesis, erect in fruit, white or pale green; peduncles 5–15 mm long; rachis 4.5–9 cm long, < 5 mm thick. Floral bracts subtriangular to rounded-peltate, 0.2–0.3 mm wide, fimbriate and pilose adaxially. Fruit obpyramidal or oblong-cylindrical, 1–1.3 mm long, apiculate, apically papillate-puberulent.

Found in Central America and South America (Colombia, Venezuela, and Ecuador). Widespread in Venezuela (Aragua, Barinas, Cojedes, Dependencias Federales, Distrito Capital, Falcón, Lara, Mérida, Miranda, Portuguesa, Trujillo, Vargas, Yaracuy, and Zulia; Map 80). In the park, collected along the Boconó–Guaramacal road; 2,000–2,200 m.

♦ ***Piper calvarii*** S. M. Niño & Dorr, Harvard Pap. Bot. 23: 11, fig. 2. 2018.

**MAP 80.** Distribution of *Piper bredemeyeri.*

FIGURE 7

Shrubs, 1–2 m tall; stems smooth, terete, striate, with scattered glandular dots; nodes glabrous, prominent, almost always with stipular scars. Leaf blades linear-lanceolate or lanceolate, 4–9 × 1.5–2.3 cm, base obtuse or acute, equilateral or oblique on the same branch, both sides acute or subacute, when oblique the unequal lobe generally 0.5–1 mm shorter than the other one, apex long acuminate, pinnatinerved with 6–8 secondary veins each side of the midrib, first pair opposite, ascending at an angle of 45–60°, the remaining pairs alternating, midrib and secondary veins glabrous and smooth, raised above, densely or conspicuously glandular-punctate below; petioles 3–6 mm long, shortly winged, each wing inserted at the base of the leaf blade, generally glabrous; sheathing stipules almost always present at nodes of terminal branches, deltoid, 2–8 mm long, sometimes extended or curved-inrolled, glabrous, caducous. Inflorescences erect, 3–5.5 cm long, 1.5–2 mm thick; peduncles 7–11 mm long, 0.7–1 mm thick. Floral bracts ovate to orbicular, 0.4–0.5 mm long, margin fimbriate and center glabrous. Fruit (immature) subglobose or rounded apically, glabrous, smooth.

Known only from the Andes of Venezuela (Trujillo; Map 81). At present, all records of this species are from the park, where it has been collected on both slopes of Guaramacal including the Fila de Los Recortaderos; 1,800–2,200 m.

This species is easily distinguished by its small (4–9 × 1.5–2.3 cm) narrowly lanceolate and acuminate leaves, and by its small stipules arising from the sheath formed between the stem and petiole.

***Piper diffamatum*** Trel. & Yunck., Piperac. N. South Amer. 1: 360, fig. 327. 1950; Steyermark, Fl. Venez. 2(2): 399–407, fig. 55, A1, B1, C1. 1984.

*Piper naiguatanum* var. *bullatifolium* Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 1: 196, fig. 155. 1950.

*Piper diffamatum* var. *angustius* Steyerm., Fl. Venez. 2(2): 402. 1984.

Shrubs, 2–4 m tall; stems glabrous, slightly pilose on upper branches. Leaves usually distichous; leaf blades ovate to elliptic-lanceolate or narrowly elliptic-ovate, 8–15 × 3–8(–10) cm, base oblique, ± cuneate or obtuse, larger lobe up to 5 mm longer than shorter one, margin crenulate, apex long acuminate, pinnatinerved with 6–7 secondary veins each side of the midrib, ascending, strongly rugose to bullate or verrucose and glabrous or midrib sparsely pilose above, alveolate below with areoles pilose toward the edge, coriaceous or subcoriaceous; petioles 5–25 mm long, sheathing, scattered pilose or glabrous; stipules prominent, foliaceous, persistant at upper nodes, lanceolate, 1–1.5(–3) cm long, obtuse, mostly glabrous or pilose dorsally, ciliate. Inflorescences erect or slightly curved; peduncles 1–3.5 cm long, sparingly pilose or glabrous, sheathing; spikes 2.5–9 cm long, cream or greenish, apiculate. Floral bracts rounded or narrowly elliptic, margins densely fimbriate. Fruit obovoid or subglobose, 1–1.2 mm in diameter, apex truncate.

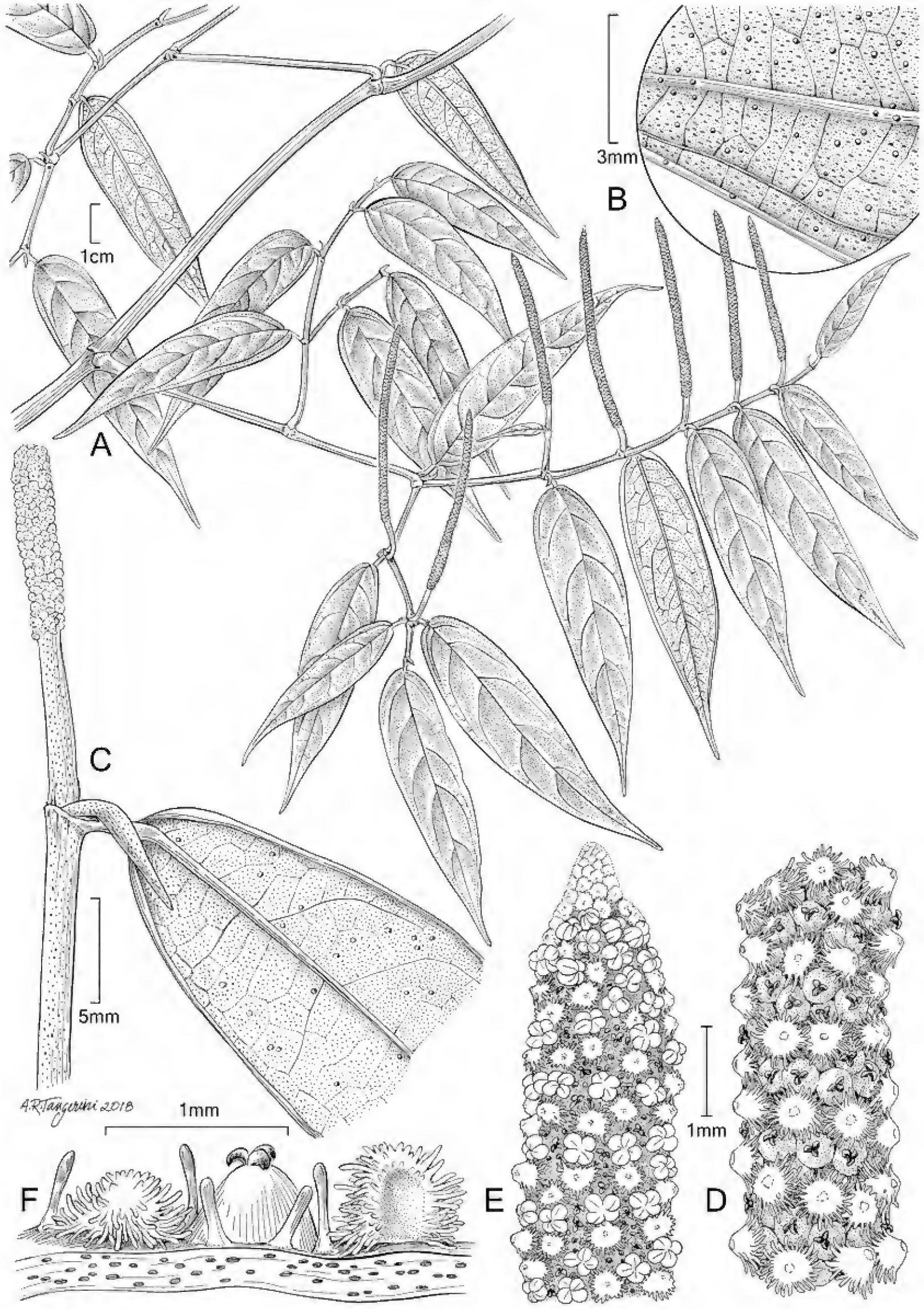



**FIGURE 7.** Piperaceae, *Piper calvarii* S. M. Niño & Dorr. **A.** Habit. **B.** Detail of undersurface of leaf showing venation and glands. **C.** Node showing leaf, intravaginal stipule, and the base of a spike. **D.** Part of an infructescence (stamens) with densely fimbriate bracts. **E.** Apical part of an inflorescence. **F.** Fruit and bracts (lateral view). (Illustrator A. R. Tangerini; A–F, *Dorr et al. 8890*).

**MAP 81.** Distribution of *Piper calvarii.*

Found in northern South America (Colombia and Venezuela). In Venezuela, known from disturbed sites or clearings in cloud forest in the Andes (Lara, Mérida, Táchira, and Trujillo) and in the Cordillera de la Costa (Falcón; Map 82). In the park, found in Sector El Campamento, below Cerro El Diablo; 1,800–2,000 m.

The strongly rugose-bullate or verrucose leaves set this species apart from all other species of *Piper* encountered in Guaramacal.

We follow Steyermark (1984) in considering *Piper naiguatanum* var. *bullatifolium* to be a synonym of *P. diffamatum*.

**MAP 82.** Distribution of *Piper diffamatum.*

***Piper dilatatum*** Rich., Actes Soc. Hist. Nat. Paris 1: 105. 1792 ("*Dilatatum*"); Steyermark, Fl. Venez. 2(2): 403–409, 411–415, fig. 56 A2, B2, C2, D2. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 719. 2003; Duno de Stefano and Aymard, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 622. 2007.

*Piper guayranum* C. DC., J. Bot. (Morot) 4: 397. 1890 ("*Guayranum*"). *Piper dilatatum* f. *guayranum* (C. DC.) Steyerm., Fl. Venez. 2(2): 407. 1984; Bono, Fl. Veg. Táchira 740. 1996.

*Piper tobagoanum* C. DC., in Urban, Symb. Antill. 3: 199. 1902.

*Piper tobagoanum* var. *humilior* C. DC., in Urban, Symb. Antill. 3: 199. 1902 ("var. β *humilior*"). *Piper guayranum* var. *humilior* (C. DC.) Trel. & Yunck., Piperac. N. South Amer. 1: 302. 1950.

*Piper margaritanum* C. DC., Proc. Amer. Acad. Arts 3: 199. 1902.

*Piper regresivanum* Trel. & Yunck., Piperac. N. South Amer. 1: 239, fig. 207. 1950. *Piper dilatatum* f. *regresivanum* (Trel. & Yunck.) Steyerm., Fl. Venez. 2(2): 411. 1984.

*Piper dilatatifolium* Trel. & Yunck., Piperac. N. South Amer. 1: 267, fig. 232. 1950. *Piper dilatatum* f. *dilatatifolium* (Trel. & Yunck.) Steyerm., Fl. Venez. 2(2): 406. 1984; Ortega et al., BioLlania 5: 52. 1987; Bono, Fl. Veg. Táchira 740. 1996; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 377. 2010.

*Piper dilatatum* f. *longipilum* Steyerm., Fl. Venez. 2(2): 412. 1984.

*Piper dilatatum* f. *taboganum* auct., non (C. DC.) Steyerm.; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 374. 2010 (as to *Licta & Niño 334*).

Shrubs, 1–2(–4) m tall; stems with older nodes enlarged; branches glabrous or sparsely to moderately pubescent. Prophylls 0.8–2 cm long, pubescent. Leaves usually distichous; leaf blades subrhomboid, obovate-elliptic or elliptic-ovate, (6–)8–20 × (3–)4–10 cm, base oblique, one lobe 1–5 mm shorter than the other lobe, margin entire, apex acuminate, glabrous and smooth above except midrib and secondary veins minutely puberulent, midrib and secondary veins pilose-pubescent below, pinnatinerved, 4–5 secondary veins each side of the midrib, secondary veins ascending, impressed above, prominent below, membranous; petioles 4–15(–20) cm long, sheathing near the base, scattered or densely pilose below. Inflorescences erect, white; peduncles 3–15 mm long, scattered puberulous or glabrous; rachis 5–11 cm long, 2–3 mm thick. Floral bracts subtriangular, 0.5–0.8 mm long, margins densely fimbriate. Fruit triangular or obpyramidal, 0.5–0.8 mm long, apically truncate, mostly glabrous. Fruit trigonous to obpyramidal, mostly glabrous.

Found in the West Indies and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, and Paraguay). Widespread in Venezuela (Amazonas, Anzoátegui, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Distrito Capital, Falcón, Lara, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Vargas, Yaracuy, and Zulia; Map 83). In the park, found in cloud forest on both slopes of Guaramacal; 1,600–2,000 m.

The stems are fragrant when cut.

In treating *Piper dilatatum*, Steyermark (1984) subdivided the species into six forms based principally on pubescence. We have reduced all but one of these to synonyms of *P. dilatatum*. The one

**MAP 83.** Distribution of *Piper dilatatum*.

form we exclude, *P. dilatatum* f. *taboganum* (C. DC.) Steyerm., is a synonym of *P. pseudofuligineum* C. DC. according to Tebbs (1993b). The basionym of this form, *P. taboganum* C. DC., was based on a collection made on Taboga Island, which is on the Pacific Coast of Panama, and its specific epithet is easily confused with that of *P. tobagoanum*, based on a collection made on the island of Tobago, which is in the Caribbean northeast of Trinidad.

The presence of *Piper dilatatum* in Central America needs to be re-evaluated. Although Steyermark (1984) and Steyermark and Callejas-Posada (2003) included Central America in its distribution, Callejas (2014) excluded the species from Costa Rica and by implication from all Central America.

***Piper hispidum*** Sw., Prodr. 15. 1788; Steyermark, Fl. Venez. 2(2): 442–453, fig. 63, A2, B2, C2, D2, E2, F2. 1984; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 720. 2003; Duno de Stefano and Aymard, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 622. 2007.

*Artanthe asperifolia* f. *surinamense* Miq., Syst. Piperac. 442. 1843 [1844]. *Piper hispidum* f. *surinamense* (Miq.) Steyerm., Fl. Venez. 2(2): 448. 1984; Bono, Fl. Veg. Táchira 741. 1996; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 378. 2010.

*Piper hispidum* var. *obliquum* Trel. & Yunck., Piperac. N. South Amer. 1: 273, fig. 236. 1950.

*Piper hispidum* var. *lanceolatum* Trel. & Yunck., Piperac. N. South Amer. 1: 274, fig. 237. 1950. *Piper hispidum* f. *lanceolatum* (Trel. & Yunck.) Steyerm., Fl. Venez. 2(2): 449. 1984; Ortega et al., BioLlania 5: 52. 1987; Dorr et al., Contr. U.S. Natl. Herb. 40: 124. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 378. 2010.

*Piper patulipilum* Yunck., in Steyermark, Bol. Soc. Venez. Ci. Nat. 23: 84, fig. 1962. *Piper hispidum* f. *patulipilum* (Yunck.) Steyerm., Fl. Venez. 2(2): 451. 1984.

*Piper* sp. F; Dorr et al., Contr. U.S. Natl. Herb. 40: 125. 2000 [2001].

Shrubs or small trees, 1–4.5 m tall; stems branched, striate, glabrescent or with light brown to ferruginous hairs 0.2–0.5 mm long, pellucid-punctate, glandular. Prophylls 1.5–1.8 cm long, densely hispid, sometimes glabrescent. Leaves mostly distichous, uniform the length of the axes; leaf blades asymmetric, lanceolate or elliptic-lanceolate, occasionally obovoid, 8–18(–23.5) × 4–10.5 cm, base oblique, the larger lobe obtuse, the smaller cuneate, occasionally both lobes cuneate, apex acuminate, densely punctate-glandular above and below, strigose or hispid above, appressed hispid, strigose below, pinnatinerved with 4–5 secondary veins each side of the midrib, veins impressed above, raised and prominent below; petioles 0.3–2.5 cm long, densely strigose; stipules prominent, 6–8 mm long, sheathing at the base. Inflorescences erect, yellowish-white or white, pale green in fruit; peduncles 5–19 mm long, hispid-strigose, glabrescent; rachis 4.5–10 cm long, < 5 mm thick, glabrous. Floral bracts triangular, 0.2 mm wide, dorsally and marginally fimbriate. Fruit obovoid, 0.6–0.8 mm long, obtuse apically, pubescent.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Brazil, Paraguay, and Argentina). Widespread in Venezuela, including the Andes (Lara, Mérida, Portuguesa, Táchira, and Trujillo), the Sierra de Perijá (Zulia), the Cordillera de la Costa (Aragua, Carabobo, Distrito Capital, Falcón, Miranda, Sucre, and Yaracuy), Nueva Esparta, the Venezuelan llanos (Anzoátegui, Apure, Barinas, and Cojedes), and the Venezuelan Guayana (Amazonas, Bolívar, and Delta Amacuro; Map 84). In the park, collected in cloud forest on both slopes of Guaramacal, including near La Divisoria de la Concepción and in the karst area above the Río Amarillo; (1,200–)1,500–2,300 m.

COMMON NAME. Cordoncillo.

We dispense here with the varieties and forms recognized by Steyermark (1984) and accept a more broadly conceived

**MAP 84.** Distribution of *Piper hispidum*.

*Piper hispidum*, which is the treatment adopted by Steyermark and Callejas-Posada (2003) and Callejas (2008). Tebbs (1993b) stated that this is "probably the most confused and confusing of the taxa in [*P.* sect. *Radula* Miq.] and often difficult to identify, especially without mature inflorescences." The scabrous leaves and erect, white inflorescences set *P. hispidum* apart from other *Piper* species in Guaramacal.

***Piper longispicum*** C. DC., Bot. Jahrb. Syst. 40: 248. 1908.

Two varieties are accepted. The material collected in Guaramacal can be referred to the following one.

***Piper longispicum*** *var.* ***glabratum*** (Yunck.) Steyerm., Fl. Venez. 2(2): 471, fig. 68. 1984. *Piper nobile* var. *glabratum* Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 1: 150. 1950.

FIGURE 6E

*Piper boconoense* Trel. & Yunck., Piperac. N. South Amer. 1: 114, fig. 87. 1950; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 377. 2010.

*Piper* sp. I; Dorr et al., Contr. U.S. Natl. Herb. 40: 125. 2000 [2001].

Shrubs or small trees, 2–10 m tall; glabrate. Leaves large; leaf blades broadly ovate to oblong-ovate, 15–35 × 6–20 cm (at widest point), base generally oblique, cordate, or obliquely-cordiform, the basal lobes not profound, sinus open, margin revolute, apex obtuse to acute, ± rugose-verrucose and glabrous above, minutely rugose-papillate and glabrous below, pinnatinerved with 4–6 secondary veins each side of the midrib, midrib sulcate above, elevated below, coriaceous; petioles 3–7 cm long, purple, wine-red, or pink, sheathing-winged, wing extending up to 10 mm above the base of the leaf, glabrous. Inflorescences green or brown to dark brown at maturity, pendulous, spikes with rachis 10–40 cm long, 4–10 mm thick; peduncles 1–3.5 cm long, glabrous or glabrescent. Floral bracts concave-cucullate, apex rounded, ciliate or fimbriate. Fruit ovoid, 0.2–0.3 mm long, slightly angled, depressed in the center, glabrous.

Restricted to northern Andean South America (Colombia and Venezuela). In Venezuela, known only from the Andes (Lara, Mérida, Portuguesa, Táchira, and Trujillo; Map 85). In the park, found in cloud forest on both slopes of Guaramacal, including the karst area above the Río Amarillo; (1,200–)1,500–2,300(–3,000) m.

The very long pendulous inflorescences, arborescent habit, and large leaf blades make this *Piper* easy to recognize in the field. Our variety, *P. longispicum* var. *glabratum*, is weakly distinguished from the nominate one. The leaves below are glabrous rather than pubescent or tomentose. *Piper longispicum* var. *longispicum* has a slightly more extensive distribution than our variety and also occurs in Central America (Costa Rica and Panama) and Ecuador.

***Piper morii*** (Steyerm.) Dorr & S. M. Niño, **comb. et stat. nov.** *Piper subsessilifolium* var. *morii* Steyerm., Fl. Venez. 2(2): 567, fig. 88 [sphalm., the correct image (but not the correct caption) is fig. 87 A–C]. 1984; Bono, Fl. Veg. Táchira 744–745. 1996.

**MAP 85.** Distribution of *Piper longispicum* var. *glabratum*.

FIGURE 6F–H

*Piper subsessilifolium* auct., non C. DC.; Dorr et al., Contr. U.S. Natl. Herb. 30: 125. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 379. 2010.

Hemiepiphytic lianas; 1–3 m long, branched; creeping or occasionally decumbent; stems green or reddish, striate or slightly channeled when dry; rooting from nodes. Prophylls 2–6 cm long, dorsally hirsute, glabrescent, caducous. Leaves distichous, variable in shape and size along an axis; leaf blades ovate, elliptic-ovate, or elliptic-lanceolate, sometimes widely ovate, symmetrical or asymmetrical, 7.5–20 × 2.5–10 cm, base oblique, rounded-cordate, apex acuminate to long-acuminate, pellucid-punctate below, glabrous or hirtellous on both surfaces, pinnatinerved with 4–6 secondary veins each side of the midrib, ascending, subequidistant and ± parallel, midrib and secondary veins impressed and slightly sulcate above, secondary and tertiary veins prominent below, glabrous above except for the basal part of the midrib with small appressed hairs, older leaves completely glabrous below; petioles 3–7 mm long, retrorsely ciliate on apical margins, somewhat sheathing basally; stipules prominent at nodes, 4–9 mm long, caducous. Inflorescences erect, red-purple or violet; peduncles 0.3–1 cm long, hirsute or glabrescent; rachis 3–7.5 cm long, glabrous. Floral bracts narrowly triangular, 0.3 mm wide, densely fimbriate. Fruit obpyramidal, 0.4 mm long, truncate and depressed apically, glabrous.

Found in northern South America where it occurs in Venezuela, but also is expected to occur in Colombia. In Venezuela, known from the Andes (Táchira and Trujillo) and the Cordillera de la Costa (Falcón and Yaracuy; Map 86). In the park, collected in cloud forest on the north slope of Guaramacal; 1,850–2,100 m.

This species is easy to recognize because it is the only hemiepiphyte among the species of *Piper* found in the park.

**MAP 86.** Distribution of *Piper morii.*

*Piper morii* differs from *P. subsessilifolium* C. DC., which was described from Costa Rica, in having oblique, rounded-cordate (versus ± equal, obtuse and sometimes rounded) leaf bases as well as in having a smooth (versus slightly bullate) upper leaf surface.

There is an error in the protologue (Steyermark, 1984) of *Piper subsessilifolium* var. *morii*. The captions for Steyermark's figures 88 and 87 were transposed. The image that corresponds with the new variety is on page 565 sub "Figura 87" while the correct caption is on page 568 sub "Figura 88."

***Piper neovenezuelense*** M. A. Jaram., PhytoKeys 227: 17. 2023, stat. et nom. nov. *Piper veraguense* var. *venezuelense* Steyerm., Fl. Venez. 2(2): 590. 1984; Ortega et al., BioLlania 5: 53. 1987; Dorr et al., Contr. U.S. Natl. Herb. 40: 125. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 379–380. 2010.

FIGURE 8A,B

Shrubs or small trees, 2–5 m tall; erect; stems glabrous; upper internodes 4–14 cm long; sometimes rooting at the nodes. Prophylls to 2 cm long, glabrous. Leaves peltate; leaf blades broadly lanceolate-oblong to ovate or suborbicular-ovate, 10–30 × 9–18 cm, base subcordate or rounded, petioles inserted 3–4 cm from the margin of the leaf base below, apex subcaudate, generally with 8–10 secondary veins arising from the base and 2–3 pinnate veins arising from each side of the midrib, slightly rugose and glabrous above, midrib and principal veins pilose below, chartaceous or membranous; petioles 3–7 cm long, glabrous, sheathing. Inflorescences erect, spikes green, cream, or rarely dark violet; peduncles 1.5–3.5 cm long, glabrous; rachis of the spike 10–16 cm long. Floral bracts rounded-subrhombic, apex convex, margins sparingly fimbriate. Fruit obovoid, trigonous or subquadrangular, 0.8–1 mm in diameter, glabrous or sparingly papillate apically.

Endemic to Venezuela where it is restricted to the Andes of Venezuela (Barinas, Mérida, Portuguesa, Táchira, and Trujillo; Map 87). In the park, growing in cloud forest on both slopes of Guaramacal; 1,600–2,100 m.

Among the species of *Piper* known from Guaramacal this species is easily recognized by its distinctive peltate leaves that hang vertically from the petiole. Steyermark (1984) proposed several varieties based on leaf pubescence, but Tebbs (1990) noted that inasmuch as leaf pubescence varies throughout the range of the species and is not correlated with geography there was no basis for recognizing varieties. Jaramillo et al. (2023), however, while recognizing that the various taxa might form a species complex, chose to recognize the Venezuelan element at species rank.

***Piper oblongum*** Kunth, in H. B. K., Nov. Gen. Sp. [fol.] 1: 52. 1815 [1816]; ibid. [qu.] 1: 44. 1815 [1816]; Steyermark, Fl. Venez. 2(2): 501–502, fig. 74, A2. 1984.

Shrubs, 1–3 m tall; stems with prominent nodes, glabrous or inconspicuously and sparsely appressed pubescent. Leaves distichous; leaf blades elliptic or lanceolate-elliptic, 8–13.5 × 2.5–6 cm, base slightly oblique, obtuse or rounded, apex long acuminate, not falcate, completely glabrous above, glabrous and sparsely puberulent below, midrib and lateral veins hirtellous or sparingly puberulent, pinnatinerved with 3–5 faint secondary veins each side of the midrib, the basal ones more branched and ascending, membranous; petioles 3–7 mm long, glabrous or slightly puberulous toward the apex, sheathing at the base; stipules small, 5–15 mm long, lanceolate, glabrous except dorsal keel and margins ciliate. Inflorescences erect, cream-colored; peduncles 8–12 mm long, glabrous or fimbriate; rachis 6–10 cm long, 2–4 mm thick. Fruit obpyramidal-trigonous, glabrous.

Restricted to South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, found in the Andes (Lara, Portuguesa, Táchira, and Trujillo) and the Cordillera de la Costa (Sucre; Map 88). In the park, a single collection was made in cloud forest at an unspecified location between Boconó and the village of Guaramacal; 2,100–2,300 m.

Reports of this species occurring in Mexico, a significant disjunction, appear to be based on misidentifications (McKown, 1928).

***Piper pervenulosum*** Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 1: 376, fig. 336. 1950.

*Piper aequale* var. *glanduligerum* auct., non (C. DC.) Steyerm.; Steyermark, Fl. Venez. 2(2): 314. 1984 (excluding type); Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 376. 2010.

Shrubs, 3–4 m tall; decumbent climbers; stems 1–1.5 mm in diameter with prominent nodes, glabrous. Leaves generally distichous; leaf blades oblong-ovate, 12–24 × 5–8.5 cm, base oblique to ± truncate, one lobe usually slightly longer than the other, apex short or long acuminate, apical tip 0.5–3 cm long, glabrous above and below, pinnatinerved with 6–10 secondary veins

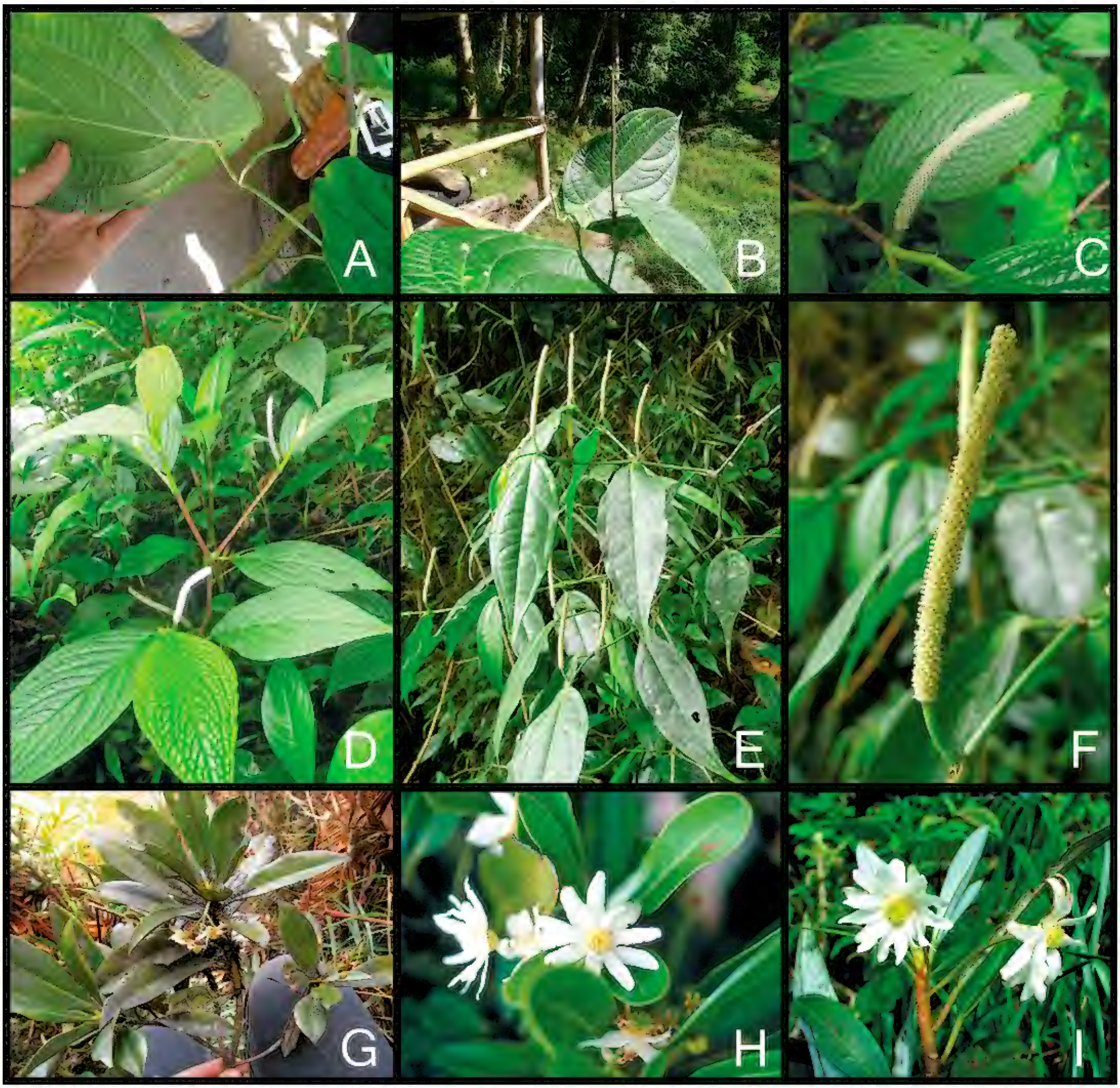



**FIGURE 8. A, B.** Piperaceae, *Piper neovenezuelense* M. A. Jaram. A. Peltate leaf blade below. B. Peltate leaf blade above and erect inflorescence. **C, D.** *P. prunifolium* J. Jacq. var. *prunifolium*. C. Inflorescence. D. Habit. **E, F.** *P. sotobosquense* S. M. Niño & Dorr. E. Habit. F. Infructescence. **G–I.** Winteraceae, *Drimys granadensis* L. f. G. Habit. H, I. Flowers. (A–G, photographer D. Canelón; H, I photographer L. J. Dorr).

on each side of the midrib, tertiary veins numerous, reticulate, deep green above, paler dull green below (drying almost black), subcoriaceous to firmly membranous; petioles 6–18 mm long, channeled. Inflorescences erect, spikes 4.5–7 cm long, 3–4.5 mm thick, white (green when immature); peduncles 5–15 mm long, glabrous. Floral bracts cucullate-inflexed, apex somewhat convex. Fruit obpyramidal-trigonous, 1–1.2 mm long, glabrous.

Endemic to Venezuela where it is known only from the Andes (Mérida and Trujillo; Map 89). In the park, found in cloud forest on the north slope of Guaramacal; 1,800–2,000 m.

MAP 87. Distribution of *Piper neovenezuelense*.

Steyermark (1984) argued that *Piper pervenulosum* is simply a large-leaved form of *P. aequale* var. *glanduligerum* (C. DC.) Steyerm. (≡ *P. glanduligerum* C. DC.) and, in fact, the two taxa differ in size: the leaves of the former are 10–15 cm wide or wider while those of the latter are 5–8.5 cm wide. He also noted similarities in the venation of the two taxa. Admitting these similarities, the two taxa nonetheless have very different leaf bases: those of *P. pervenulosum* are oblique to ± truncate while those of *P. glanduligerum* (≡ *P. aequale* var. *glanduligerum*) are ± equal. Also, as noted above, Tebbs (1990) considered *P. glanduligerum* (≡ *P. aequale* var. *glanduligerum*) to be a synonym of *P. schiedeanum*.

MAP 88. Distribution of *Piper oblongum*.

MAP 89. Distribution of *Piper pervenulosum*.

*Piper pervenulosum* also is similar to *P. aequale* but can be distinguished by leaf venation. The former species has 6–10 secondary veins each side of the midrib and its tertiary veins are pronounced and reticulate. The latter species has only 4–6 secondary veins each side of the midrib and its tertiary venation is finely reticulate and inconspicuous.

***Piper phytolaccifolium*** Opiz, in C. Presl, Reliq. Haenk. 1(3): 151. 1828 ("*phytolaccaefolium*"); Steyermark, Fl. Venez. 2(2): 521–528, fig. 79, A3, B3, C3, D3, E3, F3. 1984 ("*phytolaccaefolium*"); Duno de Stefano and Aymard, in Duno de Stefano et al., Fl. Vasc. Llanos Venez. 623. 2007.

*Peltobryon attenuatum* Klotzsch ex Miq., Syst. Piperac. 371. 1843 [1844], non *Piper attenuatum* Buch.-Ham. ex Miq., Syst. Piperac. 306. 1843 [1844]. *Piper peltobryon* C. DC., in de Candolle, Prodr. 16(1): 259. 1869 ("*Peltobryon*"), nom. nov. *Piper phytolaccifolium* var. *peltobryon* (C. DC.) Trel. & Yunck., Piperac. N. South Amer. 1: 52. 1950 ("*phytolaccaefolium*"). *Piper phytolaccifolium* f. *peltobryon* (C. DC.) Steyerm., Fl. Venez. 2(2): 526. 1984 ("*phytolaccaefolium*"); Bono, Fl. Veg. Táchira 743. 1996 ("*phytolaccaefolium*").

Two varieties occur in Venezuela. Only the nominate one is found in Guaramacal.

### *Piper phytolaccifolium* var. *phytolaccifolium*

Shrubs or small treelets, 0.8–5 m tall; stems glabrous, glandular dotted. Prophylls 1–2.5 cm long, glabrous. Leaves distichous; leaf blades narrowly to broadly lanceolate or oblong-elliptic, 8–18 × 2.5–6 cm, base acute or obliquely cuneate, almost always equilateral, apex acute to short acuminate, glabrous, usually glandular dotted below, pinnatinerved with 5–7 secondary veins on each side of the midrib, membranous or papery; petioles 5–23 mm long, sheathing at the base. Inflorescences erect, almost

always pendulous in fruit, rachis of spike white, cream-colored, or green (in fruit), 1.5–3.5 cm long, 3–5 mm thick when flowering, to 10 mm thick in fruit; peduncles 1–1.8 cm long. Floral bracts triangular or rounded, margins usually fimbriate, apex puberulent to glabrous. Fruit globose, 3–3.5 × 2–2.5 mm, green (black when dry), apiculate, the apex curved, 1–2 mm long.

Found in Mexico, Central America, and South America (Colombia, Venezuela, French Guiana, Ecuador, and Peru). Widespread in western Venezuela (Aragua, Barinas, Carabobo, Cojedes, Falcón, Lara, Mérida, Portuguesa, Táchira, Trujillo, Yaracuy, and Zulia; Map 90). In the park, known from lower elevation cloud forest on the south slope of Guaramacal, including the karst area above the Río Amarillo; (1,200–)1,500–1,800 m.

*Piper phytolaccifolium* var. *phytolaccifolium* is easily recognized by its shiny glabrous leaves with yellowish glandular punctations above and below, as well as by its short and relatively thick inflorescences.

Although *Peltobryon attenuatum* is an older name than *Piper peltobryon* C. DC., a combination in *Piper* based on the former is blocked by *Piper attenuatum* Buch.-Ham. ex Miq. Tebbs (1990) considered *Peltobryon attenuatum* to be a synonym of *Piper divaricatum* G. Mey., but the inflorescences are different. She appears to have followed Yuncker (1972), who, however, qualified his synonymy by listing the name as "*Peltobryon attenuatum* Klotzsch in Miq., Syst. Pip. 371. 1844, p.p." Presumably Yuncker (1972) intended to exclude the Venezuelan element collected in Aragua state and not the Brazilian elements cited in the protologue.

*Piper phytolaccifolium* var. *caraboboense* (C. DC.) Steyerm. can be distinguished from the nominate variety by its narrower, very short-petiolate leaves, and short spikes that are only 1–1.5 cm long.

***Piper prunifolium*** J. Jacq., Ecl. Pl. Rar. 1: 140, t. 94. 1811 [1816]; Steyermark, Fl. Venez. 2(2): 532–535, fig. 80, A5. 1984.

*Piper flexuosum* J. Jacq., Ecl. Pl. Rar. 1: 139, t. 93. 1811 [1816], nom. illeg. superfl., non *Piper flexuosum* Rudge, Pl. Guian. 13, t. 13. 1805. *Piper bredemeyeri* var. *flexuosum* Trel. & Yunck., Piperac. N. South Amer. 1: 187. 1950.

*Piper fendlerianum* C. DC., J. Bot. 4: 213. 1866 ("*Fendlerianum*").

*Piper naiguatanum* Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 1: 196, figs. 154–155. 1950.

Two varieties occur in Venezuela. Only the nominate one is found in Guaramacal.

### *Piper prunifolium* var. *prunifolium*

FIGURE 8C,D

Shrubs, 1–3 m tall; stems reddish (at least apically). Prophylls lanceolate, 1.2–2 cm long, pilose. Leaf blades ovate or ovate-elliptic, 9–21 × 3–10 cm, base oblique, one side 1–3 mm shorter than the other one or sometimes equal (and then not oblique) on the same branch, subacute to rounded, apex acute to acuminate, glabrescent or slightly appressed pubescent but only below, glabrous above or almost glabrous, the midrib and secondary veins sometimes minutely puberulent, pinnatinerved with 4–5 veins each side of the midrib ascending at an angle of 45–50° from the midrib, somewhat impressed below, tertiary venation reticulate; petioles 0.8–3 cm long, glabrous or slightly ciliate, sheathing at the base. Inflorescences erect or slightly curved, white or gray at anthesis; peduncles 0.8–2 cm long, glabrous or pilose; rachis 3–4.5 cm long, 3–6 mm thick, apiculate. Floral bracts triangular to rounded-subpeltate, margins densely pale fimbriate. Fruit suborbicular, 1–1.5 mm long, glabrous.

Found in South America (Colombia, Venezuela, and Ecuador). In Venezuela, known from the Andes (Mérida, Táchira, and Trujillo) and the Cordillera de la Costa (Anzoátegui, Aragua, Distrito Capital, Miranda, and Yaracuy; Map 91). In the

**MAP 90.** Distribution of *Piper phytolaccifolium* var. *phytolaccifolium*.

**MAP 91.** Distribution of *Piper prunifolium* var. *prunifolium*.

park, our collections are from cloud forest on the north slope of Guaramacal; 1,800–2,500 m.

*Piper prunifolium* var. *carboneranum* (Yunck.) Steyerm., endemic to Venezuela, can be distinguished from the nominate variety by the indumentum on its leaf blades (appressed pubescent within the reticulate areoles formed by tertiary veins below versus glabrous or mostly glabrous) and by its petioles (sheathing at the base only versus sheathing one-third to one-half their length).

We have adopted the synonymy proposed by Callejas (2008). Other infraspecific taxa recognized by Steyermark (1984) are not included in our concept of *Piper prunifolium*. *Piper prunifolium* subsp. *artanthe* (C. DC.) Steyerm. is treated as *P. artanthe* C. DC. in Colombia (Bernal, 2016) and presumably the Venezuelan material cited by Steyermark (1984) also represents that species. *Piper prunifolium* f. *strigosum* (Trel. & Yunck.) Steyerm. also can be referred to *P. artanthe*. *Piper prunifolium* var. *tachiranum* (Yunck.) Steyerm. is treated as *P. tachiranum* Yunck. by Callejas (2008) and presently is known only from the type.

♦ ***Piper sotobosquense*** S. M. Niño & Dorr, Harvard Pap. Bot. 23: 9, fig. 1. 2018.

FIGURES 8E,F; 9

*Piper* sp. A; Dorr et al., Contr. U.S. Natl. Herb. 40: 125. 2000 [2001]; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 380. 2010 ("*Piper* sp.").

Shrubs or small trees, (0.5–)2–4 m tall; stems almost always glabrous, sometimes with appressed hairs; internodes of basal branches 5–9 cm long and of terminal branches 2–3.5 cm long. Leaf blades ovate-lanceolate or lanceolate-acuminate, 6–12(–14) × 1.5–4(–5.5) cm, base oblique, subequilateral or equilateral in some leaves on the same branch, both sides acute or subacute, the unequal side generally 1–3 mm shorter than the other, apex long acuminate, slightly falcate, appressed pubescent and slightly raised below, glabrous above and densely or conspicuously brown or almost black glandular-dotted below, pinnatinerved with 3–6 secondary veins each side of the midrib, secondary veins diverging from midrib at an angle of 30–45°, anastomosing 3–4 mm from the margin, midrib and secondary veins smooth or slightly elevated above; petioles 4–8 mm long, shortly winged, each wing inserted at the base of the blade, generally glabrous, sometimes minutely hirtellous, sheathing at the base with a 2–2.5 mm long sheath and always with a slightly elevated edge on the petiolar axis; stipules usually persistent, black when dry, curved, 3–10 mm long, almost always glabrous, sometimes hirsute, glandular. Inflorescences erect; spike green or greenish-white, rachis 3–6 cm long, 2–3 mm thick at anthesis (3–4 mm thick in fruit); peduncles 4–10 mm long, 0.8–1 mm thick. Floral bracts triangular, margins densely fimbriate. Fruit globose, subglobose, or rounded apically, 0.8–1.2 mm in diameter, somewhat depressed in the center, glabrous, smooth, sometimes verrucose.

Endemic to the Andes of Venezuela (Portuguesa and Trujillo; Map 92) where it is only known from Guaramacal National Park. In the park, found in cloud forest on both slopes of Guaramacal; 1,550–2,100 m.

**MAP 92.** Distribution of *Piper sotobosquense*.

This species is found in slightly disturbed sites, usually in the understory.

***Piper tristemon*** C. DC., in de Candolle, Prodr. 16(1): 328. 1869; Steyermark, Fl. Venez. 2(2): 579–581, fig. 91, A1, B1, C1. 1984.

Two varieties occur in Venezuela. Only the nominate one is found in Guaramacal.

***Piper tristemon*** var. ***tristemon***

Shrubs or small trees, 2–4 m tall; stems and young branches glabrous; all parts of plant densely covered with glandular dots. Leaves relatively large; leaf blades ovate to suborbicular-ovate, 12–21 × 9–15 cm, base equilateral or subequilateral (slightly oblique), truncate, obtuse, or rounded, slightly auriculate, sometimes appearing broadly cordate, apex rounded to acute, glabrous, pinnatinerved with 6–7 secondary veins each side of the midrib, dark green above, silvery- or glaucous-green below, subcoriaceous or membranous; petioles 4–9 cm long, sheathing to the middle, winged. Inflorescences erect or ascending, green; peduncles 1.5–3 cm long, glabrous; rachis of the spikes 3–9 cm long, 3–5 mm thick. Floral bracts triangular or suborbicular, marginally fimbriate. Fruit subtrigonous, 1.8–2.1 mm long, apex granular.

Found in northern South America (Colombia, Venezuela, and Ecuador). In Venezuela, known from the Andes (Mérida and Trujillo) and the Cordillera de la Costa (Aragua and Distrito Capital; Map 93). In the park, collected in cloud forest on the south slope of Guaramacal; 1,900–2,600 m.

*Piper tristemon* var. *pilosum* Trel. & Yunck., described from Mérida state, can be distinguished from the nominate variety by the retrorse pubescence of its distal internodes, the abundantly appressed-puberulent leaf blades above and below, and by its larger leaves (25 ×18 cm). *Piper tristemon* var. *tristemon*

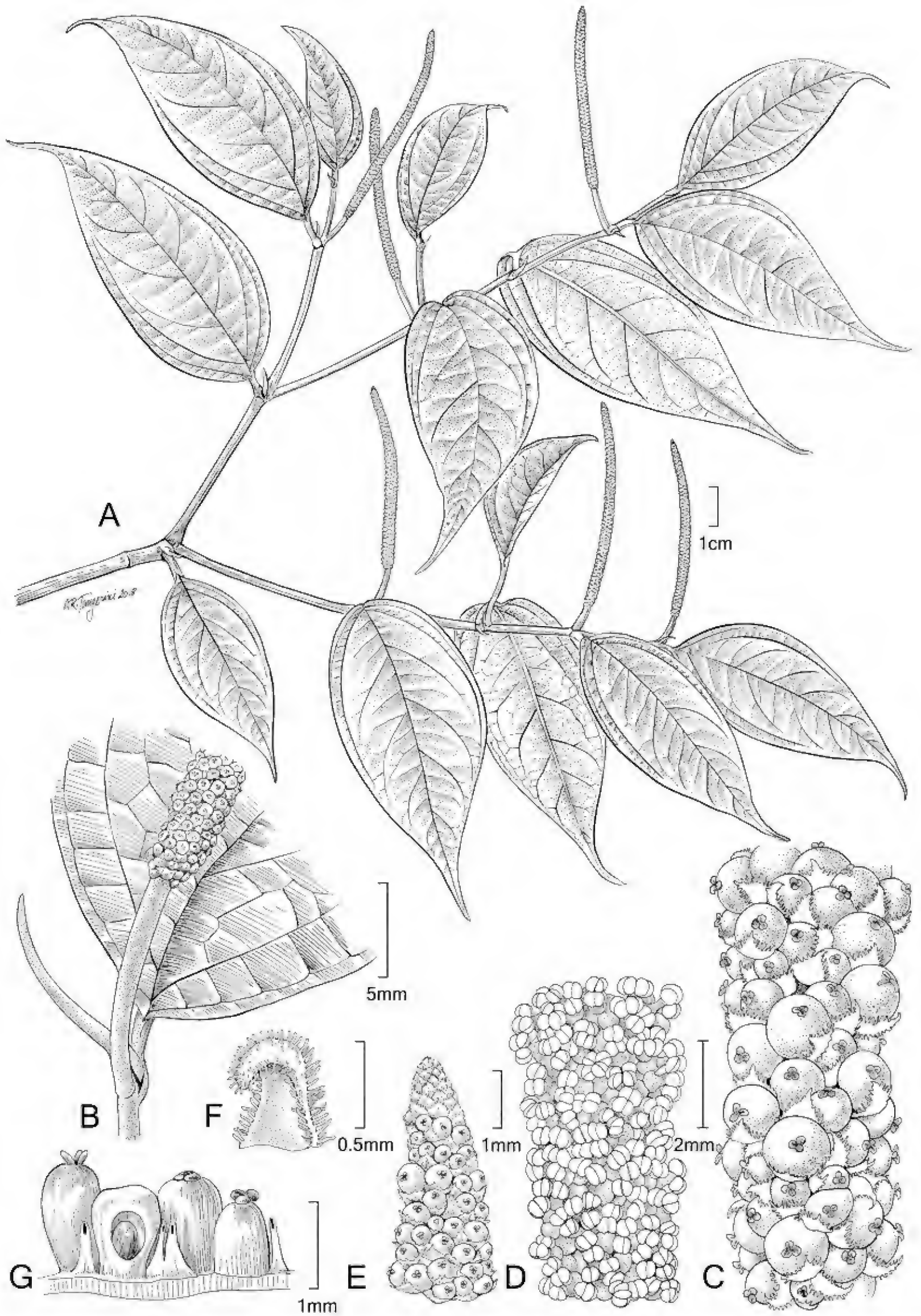



**FIGURE 9.** Piperaceae, *Piper sotobosquense* S. M. Niño & Dorr. **A.** Habit. **B.** Base of leaf, prophyll, and inflorescence opposite the leaf. **C.** Part of an infructescence. **D.** Part of an inflorescence (stamens). **E.** Apical part of an inflorescence. **F.** Floral bract. **G.** Fruit (lateral view). (Illustrator A. R. Tangerini; A–C, E–G, *Dorr et al. 8136*; D, *Dorr & Yustiz 8539*).

**MAP 93.** Distribution of *Piper tristemon* var. *tristemon*.

is glabrous and only occasionally has appressed and minute (not ciliate) pubescence on the secondary and tertiary veins on the leaf blades below.

***Piper umbellatum*** L., Sp. Pl. 30. 1753; Steyermark and Callejas-Posada, in Berry et al., Fl. Venez. Guayana 7: 726. 2003. *Pothomorphe umbellata* (L.) Miq., Comm. Phytogr. 36. 1840; Steyermark, Fl. Venez. 2(2): 602–606, fig. 95, A1, B1, C1, D1, E1. 1984.

*Piper umbellatum* var. *glabrum* C. DC., in de Candolle, Prodr. 16(1): 333. 1869 ("γ, *glabrum*"). *Pothomorphe umbellata* var. *glabra* (C. DC.) Trel. & Yunck., Piperac. N. South Amer. 2: 440. 1950; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 380. 2010. *Pothomorphe umbellata* f. *glabra* (C. DC.) Steyerm., Fl. Venez. 2(2): 604. 1984.

Subherbaceous or soft stemmed shrubs, 0.3–2 m tall; stems pale green, striate, pellucid-punctate or glabrescent; internodes 2–7 cm long. Prophylls 1–2 cm long, glabrous, caducous. Leaves uniform the entire length of a shoot, very large; leaf blades symmetric, widely ovate, 9–25(–40) × 11–42 cm, base deeply and widely cordate with rounded subequal lobes, apex shortly acute to obtuse, ± puberulent above and below, pellucid punctate above and below, green-opaque above, pale green below, palmatinerved with 7–14 secondary veins each side of the midrib, secondary veins impressed above, raised and prominent below, membranous; petioles 10–30 cm long, sheathing, retrorse-puberulent or pilose, eventually glabrescent; stipuliform margins to 5 mm long. Inflorescences compound, axillary, umbellate spikes on a common penduncle 0.5–2.5 cm long, spikes 2–14 and subadjacent to 1–2 cm long bracts, caducous, glabrous; peduncles 0.6–0.8 cm long; rachis 6–10 cm long, glabrous. Floral bracts widely triangular, subpeltate, marginally fimbriate. Fruit obovoid or trigonous, 0.2–0.3 mm long, truncate apically, depressed centrally, glabrous.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, Guyana, Suriname, Ecuador, Peru, Bolivia, and Brazil); introduced in Africa, Madagascar, Asia, and Australia. Widespread in Venezuela (Anzoátegui, Aragua, Bolívar, Carabobo, Cojedes, Distrito Capital, Falcón, Guárico, Lara, Miranda, Monagas, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, and Zulia; Map 94). Known from secondary-primary forest transition in the karst area above the Río Amarillo near the lower boundaries of the south slope of the park; 1,200–1,400 m.

***Piper viridistachyum*** Yunck., in Trelease and Yuncker, Piperac. N. South Amer. 1: 18. 1950; Steyermark, Fl. Venez. 2(2): 592, 594, fig. 93, A3, B3, C3, D3. 1984.

Shrubs or small trees, 2–4 m tall; apical internodes 6–15 cm long; retrorsely appressed pubescent on the upper branches; lower nodes glabrescent. Apical prophyll 2.5–3.5 cm long, glabrescent. Leaf blades widely-ovate to suborbicular, 10–25 × 8–14 cm, base oblique, rounded, truncate, or cordiform, apex acuminate, hirtellous above and below with veins appressed pubescent, green above, pale- or silvery-green below, pinnatinerved with 6–8 secondary veins each side of the midrib, tertiary venation almost always rugose below, subcoriaceous or firmly membranous; petioles 3–8 cm long, sheathing at the base, pilose or retrorsely pubescent. Inflorescences obliquely ascending; peduncles 1–2.5 cm long; spikes 10–14.5 cm long, 6–10 mm thick, green, hirtellous or glabrescent. Floral bracts triangular-peltate, 1–1.2 mm long, margins fimbriate. Fruit globose or cylindrical-oblong, sometimes obpyramidal, 2–2.5 × 1–1.5 mm, subrugose, glabrous.

Found in northern South America (Colombia and Venezuela). In Venezuela, restricted to the Andes (Mérida, Táchira, and Trujillo; Map 95). In the park, found in cloud forest on both slopes of Guaramacal and on the Fila de Agua Fría; 2,200–2,800 m.

**MAP 94.** Distribution of *Piper umbellatum*.

MAP 95. Distribution of *Piper viridistachyum*.

*Piper nubigenum* var. *venezuelense* Steyerm., which was attributed to the flora of Guaramacal by Ortega et al. (1987), is excluded here. The voucher (*Vareschi 6466*, VEN) cited is from the Páramo de Boconó (i.e., the Páramo de La Cristalina in Dinira National Park), which is to the northeast of Guaramacal National Park.

## SIPARUNACEAE

S. MIGUEL NIÑO AND L. J. DORR

Monoecious or dioecious trees and shrubs; aromatic, volatile oil in oil cells present throughout. Leaves simple, opposite, decussate, or 3-, 4- or 6-verticillate; leaf blades sparsely or densely pubescent, margin serrulate, dentate or entire; petiolate. Inflorescences mono- or dichasial cymes, axillary and/or on leafless nodes, sometimes bifid or fasciculate. Flowers unisexual, almost always radial; pedicellate. Floral receptacle subglobose, cup-shaped; tepals 4–6(–8), sometimes fused and surrounding the receptacle, 1 tepal much longer than the others or forming a calyptra (*Glossocalyx*), the center of the flower ± covered by a membrane (floral veil or velum) except for a central pore through which stamens or styles emerge; stamens usually 5–9, scattered irregularly in the floral cup except in flowers with few stamens; anthers with longitudinal dehiscence or pores (valvular); carpels 3–35, free but completely embedded in the receptacle, sessile; styles free; stigmas papillose and decurrent; ovules solitary, united basally, anatropous. Mature fruiting receptacle fleshy, globose to elongate, crowned by persistent tepals; drupelets with a thin fleshy exocarp and mesocarp, and a stony endocarp.

A tropical family of two genera (*Glossocalyx* Benth. and *Siparuna* Aubl.) and ~50–75 species found in Mexico, Central America, the West Indies, South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, and Paraguay), and Africa. *Siparuna* is restricted to the Americas and the unispecific *Glossocalyx* is found in West Africa.

REFERENCES. Philipson (1993); Renner and Hausner (2005).

### *Siparuna* Aubl.

*Siparuna* Aubl., Hist. Pl. Guiane 2: 864. 1775.

Trees or shrubs; sometimes decumbent. Leaves almost always pubescent, hairs greatly variable structurally and morphologically; margin dentate, serrate, or entire. Inflorescences axillary or associated with nodes, mono- or dichasial cymes. Flowers pedicellate; receptacles subglobose, cup-shaped, or urceolate, with a crown or a crushed and convex veil resembling a disc, perforated at the apex, margin undulate or with 4–7 tepals or small and subequal lobes. Staminate flowers with few to many stamens enveloped by the receptacle; stamens deltoid, ovate-elliptic, broadly ligulate to cylindrical; anthers 2-locular, introrsely 2-valved. Pistillate flowers with few to many free carpels surrounded by the receptacle; styles elongated and exserted. Mature fruiting receptacles fleshy, subglobose, smooth, spiny, or tuberculate, or longitudinally ribbed, crowned by persistent tepals, red, yellow, orange, pink, or white, splitting irregularly from the apex and spreading to reveal drupelets; in most dioecious species (including our species) drupelets with an apical or lateral reddish-orange aril-like outgrowth of the style base ("stylar aril"), rarely drupelets lacking appendage and/or receptacle not opening at maturity.

Found in Mexico, Central America, the West Indies, and South America (Colombia, Venezuela, Trinidad and Tobago, the Guianas, Ecuador, Peru, Bolivia, Brazil, and Paraguay). The genus includes ~50–55 species of which 14 occur in Venezuela.

REFERENCES. Perkins (1901); Renner et al. (1997); Renner and Won (2001).

Renner and Won (2001) noted an interesting and strong correlation among sexual breeding systems, leaf margin, and elevation in this genus. Andean *Siparuna*, which are dioecious and have toothed leaves, form a clade distinct from lowland (< 700 m elevation) *Siparuna*, which are monoecious or secondarily dioecious.

***Siparuna thecaphora*** (Poepp. & Endl.) A. DC., Prodr. 16(2): 657. 1868. *Citrosma thecaphora* Poepp. & Endl., Nov. Gen. Sp. Pl. 2: 48. 1838 ("*thecaphorum*").

*Siparuna venezuelensis* Perkins, Bot. Jahrb. Syst. 28: 679. 1901.

*Siparuna manarae* Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 455, fig. 2. 1966. *Siparuna stellulata* var. *manarae* (Steyerm.) Steyerm., Pittieria 7: 17. 1978.

Trees or scandent shrubs, 2–4 m tall. Leaves opposite or 3-verticillate; leaf blades elliptic to obovate, rarely oblong or

lanceolate, 8–16 × 3.5–8 cm, base acute to obtuse, margin serrulate, apex acuminate, apical tip 0.4–1 cm long, bifid or stellate hairs above and below, sometimes glabrescent above, 6–12 secondary veins each side of the midrib, veins smooth above, slightly raised below; petioles 1–3 cm long, pubescent. Flowers in solitary cymes or in groups of 2–8, usually shorter than petioles, pubescent or slightly glabrous, yellow or cream when fresh. Staminate cymes with 3–25 flowers, 2.5–5 mm in diameter; floral veil glabrous, convex, margin 5–6-lobed; stamens 5–9, ovate-ligulate, 1.8–3 mm long. Pistillate flowers in cymes with 1–8 flowers, 3–4 mm in diameter; floral veil glabrous; carpels 6–9; styles exerted up to 1.2 mm. Fruiting receptacles obovoid to subglobose, 5–10 mm in diameter, pubescent or glabrous, smooth, pink or reddish; drupelets gray with a bright red "stylar aril."

Found in Mexico, Central America, and South America (Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil). In Venezuela, the species occurs in the Andes (Barinas, Mérida, Táchira, and Trujillo) and the Cordillera de la Costa (Aragua, Carabobo, Distrito Capital, Miranda, Sucre, and Yaracuy; Map 96). In the park, collected in cloud forest on the north slope of Guaramacal; 1,700–2,350 m.

The closed fig-like flowers with the style tips or anthers emerging from an apical ostiole are distinctive and allow one to quickly recognize this species in flower. The fresh foliage of *Siparuna theacaphora* has a strong citrus-like odor when crushed, which is a simple way of distinguishing this species from figs (*Ficus* L., Moraceae), which have similar flowers but lack a citrus-like odor. The citrus-like odor of *S. thecaphora* is less evident in dried material.

*Siparuna theacaphora* is very variable morphologically and not only has a wide geographical distribution, but also an extensive synonymy.

**MAP 96.** Distribution of *Siparuna thecaphora*.

## Winteraceae

L. J. DORR AND S. MIGUEL NIÑO

Trees or shrubs, sometimes epiphytes (not in the flora area); evergreen; glabrous, rarely with hair-like papillae or minute hairs, pellucid-punctate. Leaves alternate, simple, entire, usually spiral, subopposite, or whorled, penninerved; almost always petiolate; estipulate. Inflorescences terminal, intercalary, rarely axillary, sometimes flowers solitary, fascicled or in simple or compound umbels. Flowers bisexual or unisexual (*Tasmannia*), actinomorphic or slightly zygomorphic, red, white, or yellow; bracts or bracteoles caducous; receptacle conical, short to elongate; calyx calyptrate, rupturing early, calyx lobes or sepals 2–6; petals (0)2–many, in 1–3 whorls, entire, free or the outer ones rupturing at anthesis, imbricate; stamens 3–many, free; filaments stout, fleshy; anthers (2)4-locular, longitudinally dehiscent; thecae apical to lateral, opening by longitudinal slits; staminodes sometimes present in pistillate flowers; ovary superior, 1–many, free, rarely ± united; style minute or absent; stigma 1 per carpel or 1 per ovary; ovules 2–many, anatropous, placentation laminar. Fruit a cluster of follicles or berries, occasionally folicles united into a syncarp; seeds few to many, usually hard; endosperm copious.

A family of five genera and ~75 species found in the tropics and subtropics of Mexico, Central America, South America (Colombia, Venezuela, possibly Guyana, Ecuador, Peru, Brazil, Chile, Paraguay, and Argentina), Madagascar, Asia, Australia, and the Pacific Islands. Only *Drimys* J. R. Forst. &. G. Forst. occurs in the Americas.

References. Suh et al. (1993); Vink (1993); Doust and Drinnan (2004); Ruiz et al. (2008); Marquínez et al. (2009); Thomas et al. (2014).

### *Drimys* J. R. Forst. &. G. Forst.

*Drimys* J. R. Forst. &. G. Forst., Char. Gen. Pl., ed. 2, 83. 1776, nom. cons.

Trees or shrubs, sometimes epiphytes (not our species). Leaves alternate; coriaceous. Inflorescences terminal, pedunculate with bracteoles or sessile without bracteoles. Flowers bisexual, actinomorphic; calyx completely closed around the buds, generally falling before or during anthesis; petals 2 (or more), sometimes reduced to 1 (or none); carpels 1–24, in series, free; ovules 2-seriate. Fruit apocarpous with 1–many carpels, usually succulent or berry-like.

A Neotropical genus of five species found in Mexico, Central America, and South America (Colombia, Venezuela, possibly Guyana, Ecuador, Peru, Bolivia, Brazil, Chile, including the Juan Fernández Islands, Paraguay, and Argentina). Three species occur in Venezuela and are found at higher elevations in the Andes, the Sierra de Perijá, and the Venezuelan Guayana, including Mt. Roraima.

References. Smith (1943); Ehrendorfer et al. (1979).

Paleotropical material referred to *Drimys* by Smith (1943) and others is best recognized as the distantly related *Tasmannia*

R. Br. ex DC. (Suh et al., 1993; Doust and Drinnan, 2004; Ruiz et al., 2008; Marquínez et al., 2009; Thomas et al., 2014).

***Drimys granadensis*** L. f., Suppl. Pl. 269. 1781 ("*Granadensis*").
FIGURE 8G–I

*Drimys mexicana* DC., Syst. Nat. 1: 444. 1818 [1817] ("*Mexicana*"). *Drimys granadensis* var. *mexicana* (DC.) A. C. Sm., J. Arnold Arbor. 24: 23. 1943.

*Drimys uniflora* Turcz., Bull. Soc. Imp. Naturalistes Moscou 27(2): 280. 1854. *Drimys granadensis* var. *uniflora* (Turcz.) A. C. Sm., J. Arnold Arbor. 24: 23. 1943; Bono, Cat. Fl. Vert. Occid. Cordillera Mérida 452. 2010.

*Drimys granadensis* var. *grandiflora* Hieron., Bot. Jahrb. Syst. 20(Beibl. 49): 10. 1895 ("*granatensis*"); Bono, Fl. Veg. Táchira 828. 1996 ("*Drymis*").

*Drimys granadensis* var. *chiriquiensis* A. C. Sm., J. Arnold Arbor. 24: 25, fig. 3a. 1943.

*Drimys granadensis* var. *peruviana* A. C. Sm., J. Arnold Arbor. 24: 26. 1943.

Shrubs or small trees, 4–16 m tall; branches brownish or cinereous, sometime glaucous. Leaf blades elliptic-oblong, 4–14 × 2.5–4 cm, base attenuate or cuneate, margin entire, apex rounded or obtuse, glabrous, glaucous, 8–12 secondary veins each side of the midrib; petioles to 2.5 cm long. Flowers single, clustered at apices of branches; pedicels 2.5–5 cm long; petals white, oblong to elliptic, 5–20 mm long. Berries obovoid or ellipsoid, slightly falcate, dark purple or reddish-black, deep black when mature.

Mexico, Central America, and South America (Colombia, Venezuela, Ecuador, and Peru). In Venezuela, found in the Andes (Lara, Mérida, Táchira, and Trujillo) and in the Sierra de Perijá (Zulia; Map 97). In the park, found in the understory of cloud forest on both slopes of Guaramacal and in open areas of subpáramo; (1,500–)2,300–2,600 m.

**MAP 97.** Distribution of *Drimys granadensis*.

Smith (1943) recognized a number of varieties of *Drimys granadensis*, which here are treated as synonyms of a single variable species.

## NEW COMBINATION

### PIPERACEAE

***Piper morii*** (Steyerm.) Dorr & S. M. Niño, **comb. nov.**

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# Index of Scientific Names

Names of taxa recognized as occurring in the flora of Guaramacal are in bold type. All others either are synonyms or refer to taxa that are not present among the flora of Guaramacal. Page numbers in bold italic type indicate the start of the taxonomic account.


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